THE ROLE OF BIODIVERSITY IN PRAIRIE RESTORATION: TESTS OF THEORY AND IMPLICATIONS FOR MANAGEMENT

By

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ABSTRACT

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Biodiversity is a primary focus of conservation and restoration, because it has intrinsic value, and because it supports the ecosystem functioning that human well being ultimately depends upon. Theory and experiments support the hypothesis that greater diversity in plant communities supports greater primary productivity, nutrient cycling, invasion resistance and a range of other processes linked to the healthy functioning of ecosystems. However, most of the evidence for diversity-function relationships is from manipulations of diversity, and a limited number of environmental variables, in small-scale plots. As a result, it is unclear how diversity-function relationships will scale up to dynamic, "real-world" ecosystems, which limits the capacity to effectively manage both biodiversity and ecosystem functioning. I examined diversity-function relationships in prairie restorations, which provide an ideal scenario for bridging the gap between experimental and natural ecosystems because diversity is manipulated at large scales and across complex biotic and abiotic gradients. It is clear from experimental evidence that diversity plays a role in supporting ecosystem functioning. My findings elucidate how important diversity is at the scale of natural ecosystems, relative to both abiotic (e.g., soil properties) and biotic (e.g., dominant species) factors that are likely to covary with diversity at large scales. I also contribute directly to the practice of restoration by working in real restorations, linking variation in management actions, such as seed sowing and prescribed fire, to outcomes of immediate concern to managers, such as the relationship between native and exotic species.

For Zak and Fen, the future.

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CHAPTER ONE

INTRODUCTION

Introduction

Anthropogenic forces increasingly threaten the functioning of Earth's ecosystems and the biodiversity they support (Vitousek et al. 1997, Foley et al. 2005). Initially motivated by biodiversity conservation for its intrinsic value, ecologists have increasingly shifted their focus to how biodiversity supports the way ecosystems function, and ultimately how diversity-function relationships sustain human well-being (Hooper et al. 2005, Millennium Ecosystem Assessment 2005). Experimental evidence, bolstered by a rich body of theory (e.g., MacArthur 1955, Elton 1958, Lehman and Tilman 2000, Diaz and Cabido 2001), demonstrates that diversity plays a role in supporting many specific functions, including primary productivity (Hector et al. 1999, Tilman et al. 2001), invasion resistance (Fargione and Tilman 2005), nutrient cycling (Spehn et al. 2005), and many others. Diversity-function relationships strengthen the case for both the conservation of existing biodiversity and the restoration of biodiversity in degraded habitats (Young et al. 2005, Cardinale 2012).

However, questions remain about how diversity-function relationships will scale up from small-scale experimental communities (1-400m^2) to dynamic, "real-world" ecosystems (Cardinale 2012, Tilman et al. 2014). More studies are needed to understand how theoretical predictions play out at large scales, in naturally assembled ecosystems and across realistic biotic and abiotic gradients, in order to understand how to effectively manage both biodiversity and ecosystem functioning. Experimental evidence suggests that, the importance of diversity may surpass the importance of abiotic conditions for driving some functions (e.g., primary production; Hooper et al. 2012, Tilman et al. 2012), but strongly depend on abiotic conditions for driving other functions (e.g., stability, Hautier et al. 2014). Experiments such as BIODEPTH, which is replicated across sites spanning 25° of latitude from Greece to Sweden, often show variation in the strength and direction of diversity-function relationships, due to variation in factors like temperature and precipitation (Hector et al. 1999, Spehn et al. 2005). Diversity-function relationships may be even less predictable in natural and managed ecosystems, due to broader or more complex biotic and abiotic gradients. Aspects of community structure - diversity, dominance, and species composition – may vary both spatially and temporally, and may covary with abiotic factor that also drive function (Collins 2000, Ricklefs 2004).

It is also important to address diversity-function relationships explicitly in a management context, to better understand how to translate these results into practice. Restorations, where diversity is at least partially manipulated at large scales and across environmental gradients, provide a unique opportunity to test theory at large scales by bridging the gap between experiments and natural ecosystems (Young et al. 2005). Examining the causes and consequences of biodiversity in restorations provides an opportunity to bring ecological theory to bear on issues of immediate to concern to managers. For example, exotic species invasions are a primary challenge to the primary goals of restoration - diverse communities of native species and ecosystem functioning (Parker et al. 1999, Matthews and Spyreas 2010, Suding 2011, Vila et al. 2011). Examining the way exotic species invasions vary with the restoration of native biodiversity provides a test of diversity-function theory and at the same time leads to recommendations with direct applicability for managers (Rowe 2010). My dissertation uses a large dataset from 29 tallgrass prairie restorations in southwestern Michigan (Grman et al. 2014) to test basic ecological theory at large scales and in a real-world context, and to harness that theory to inform management of restored ecosystems. Specifically, I ask:

Chapter TWO) What is the relative importance of diversity, dominant species abundances, and environmental factors for ecosystem stability?

Chapter THREE) Can restoration decouple predicted positive correlations between native and exotic species richness?

Chapter FOUR) Can restoration manipulate the diversity and dominance of plant communities to resist exotic species invasions?

The tallgrass prairie grassland of North America, as with other grasslands worldwide, is one of Earth's most endangered ecosystems, the majority of historical prairie having been converted to productive farmland (Samson and Knopf 1994, Packard and Mutel 1997, Hoekstra et al. 2005). The continued erosion of biodiversity and functioning associated with tallgrass prairie is a consequence of extremely small patch size in fragmented habitats, and conversion to to shrubland due to the absence of natural disturbances (especially fire) (Alstad et al. 2016). As a result, prairie is now a major target of restoration across its historical range, where patches of former agricultural land are increasingly sown with native prairie seeds and managed with prescribed fire. As with any ecosystem, prairie restoration faces many challenges, including the restoration of native diversity and control of exotic invasive species (Ruiz-Jaen and Aide 2005, Rowe 2010, Suding 2011). Due to its widespread adoption as a land management practice across a wide geographic area, prairie restoration provides an opportunity to address a range of basic and applied questions in ecology (Grman et al. 2014).

Main results and significance

I combined field observations of plant community composition and environmental variation with data on management history to elucidate the links between the restoration of biodiversity and the functioning of restored prairies. My research shows that, while managers can strongly influence the restoration of diverse communities of native species, the role of biodiversity in restored prairies differs among functions, components of the plant community, and relative to a few key environmental variables. First, biodiversity was positively correlated with invasion resistance but negatively correlated with ecosystem stability. Furthermore, while diversity played a roughly equivalent role in limiting invasive species as dominant species and environmental factors, the negative effect of diversity on stability was stronger than these other drivers. The consensus of experimental evidence points toward positive diversity-stability relationships, so my finding of a negative diversity-stability relationship is especially significant. Second, the effects of environmental factors differed between the questions my research addressed, which emphasizes how scaling up predictions from ecological theory can lead to complex outcomes. For example, I found that soil moisture weakly limited both ecosystem stability and the richness of invasive species. In contrast, land use history had strong effects only on invasive species, while fire did not influence invasive species and only weakly affected stability.

My findings also have implications for land managers. Components of seed mixes were important in assembling communities of native species that resisted invasion, but the other aspect of management we assessed, prescribed fire, had at most a weak influence on any outcome. However, my research underscores the conventional wisdom that the relationship between native and exotic species is dynamic and difficult to disentangle. Native and exotic species richness were positively correlated, suggesting that efforts to restore native diversity while resisting exotic species invasions may be challenging. However, sites sown with more species at higher rates, particularly of forb species, had higher native richness than predicted from this correlation. The richness of sown species (a subset of native species, originating from seed mixes and not natural colonization) was also higher in sites sown with more species, which in turn led to reductions in invasive species (a subset of exotic species, most likely to have negative ecosystem impacts) abundances. Therefore, despite certain limitations (i.e., the inevitability of a certain richness and abundance of exotic species), the restoration of diversity, primarily via seed sowing, was linked to invasion resistance, a primary goal of managers.

CHAPTER TWO

DIVERSITY REDUCES STABILITY IN GRASSLAND RESTORATIONS

Abstract

Experimental evidence strongly suggests that local-scale biodiversity plays an important role for stabilizing ecosystem functioning. Yet, many questions remain about how diversity-stability relationships scale up to natural and managed ecosystems, where broader environmental gradients and variable community structure may modify or weaken the importance of diversity for stability. In 28 grassland restorations, we tested the relationship between plant species diversity and three measures of stability in primary production - *resistance* and *resilience* to drought, and *temporal stability*. We also examined the importance of diversity relative to other putative stability drivers, including dominant species abundances, abiotic conditions (prescribed fire and soil properties), and restoration age. Diversity was the strongest predictor of resistance and resilience, but contrary to expectations, diversity was negatively correlated with all three measures of stability. Diversity-stability relationships generally did not depend on other putative drivers, as they do in many experiments. These findings illustrate that the commonly-accepted benefits of biodiversity to stability may not consistently scale up from small-scale experiments to natural and managed ecological systems, illustrating the critical need to evaluate the relationships between biodiversity and aspects of ecosystem functioning, including stability, under real world conditions,. Increasing the predictability of these relationships will require an improved understanding of the range of conditions that lead to positive vs. negative diversity-stability relationships.

Introduction

There is a growing need to strengthen the capacity for natural habitats to sustain ecosystem functioning, given increases in both persistent (e.g., rising mean temperature) and periodic (e.g., drought) stresses (Millennium Ecosystem Assessment 2005, Smith et al. 2009, Ibanez et al. 2013). Decades of theory (e.g., MacArthur 1955, Lehman and Tilman 2000) and experiments (e.g., Tilman et al. 2006, Hector et al. 2010) suggest that the conservation or restoration of biodiversity reinforces ecosystem stability, the constancy of ecosystem functioning through time and in response to discrete perturbations (Pimm 1984, Griffin et al. 2009). Yet, it remains uncertain how diversity-stability relationships scale up from small (1-400m^2) experimental plots to natural and managed ecosystems which span hundreds or thousands of hectares and encompass broader abiotic gradients and more trophic complexity than existing experiments (Romanuk et al. 2009, Cardinale 2012, Tilman et al. 2014). Examining diversity-stability relationships in restored habitats, where diversity is manipulated at the ecosystem scale, provides an opportunity to bridge the gap in understanding from experiments to natural ecosystems (Young 2005, Suding 2011). Here, we examine the relationship between plant species diversity and the stability of primary production, a common measure of ecosystem stability, in response to drought in restored grasslands.

Plant species diversity, in particular richness, may affect several components of stability (Pimm 1984, Ives and Carpenter 2007). Here, we focus on three common measures of stability - temporal stability, resistance, and resilience of productivity (defined here as peak above-ground biomass) (Griffin et al. 2009). Richness may reduce variation in productivity over time (*temporal stability*), through both ecological and statistical mechanisms that average out the fluctuations of individual species (Lehman and Tilman 2000). Compensatory dynamics, where an increase in some species is offset by decreases in others as communities respond to environmental fluctuations or interspecific competition, should be stronger in species rich communities (Tilman et al. 1998, Lehman and Tilman 2000). The portfolio effect, where the sum of individual species' variances decreases with richness, is largely the product of statistical probability and also results in positive richness-stability relationships (Doak et al. 1998, Tilman et al. 1998). Richness may also stabilize productivity in response to discrete perturbations (*resistance*) and assist recovery from discrete perturbations (*resilience*), although theoretical and empirical support is more equivocal than for temporal stability (Loreau and Behera 1999, Griffin et al. 2009). The mechanisms may be similar, however, as species rich communities are likely to include more species tolerant of a specific perturbation (Yachi and Loreau 1999).

While relationships between plant species richness and stability have been widely explored, the relative importance of other biotic and abiotic factors for controlling stability is less certain (Hooper et al. 2005, Hillebrand et al. 2008, Tilman et al. 2014). Among potential biotic drivers, components of diversity other than richness are likely to be important. Species abundances vary in natural ecosystems (Preston 1948, Whittaker 1965, McGill et al. 2007). Greater evenness should strengthen the stabilizing effect of richness via compensatory dynamics and portfolio effects (Doak et al. 1998, Cottingham et al. 2001, Thibault and Connolly 2013), and may directly underpin stability (Hillebrand et al. 2008). At low evenness, stability may depend on how dominant species' traits align with environmental fluctuations, especially in the case of resistance and resilience to discrete perturbations (e.g., water use efficiency during a drought) (Leps et al. 1982, Polley et al. 2013, Hoover et al. 2014). As such, increasing the abundance of stable dominant species, rather than diversity, may enhance stability (Leps 2004, Polley et al. 2007, Wilsey et al. 2014). It is also necessary to understand how the importance of diversity for stability varies across abiotic gradients in natural ecosystems (Cardinale 2012, Tilman et al. 2014). For example, resource availability influences both stability and diversity (Collins 2000, Grman et al. 2010), and may modify diversity-stability relationships (Hautier et al. 2014, Xu et al. 2015, Zhang et al. 2016). Despite evidence that aspects of biotic communities - richness, evenness, and dominant species – and several environmental factors control stability, the relative importance of each remains less clear.

Ultimately, it is important to understand how diversity-stability relationships will scale from controlled, small-scale experiments to large-scale natural and managed landscapes (Cardinale 2012, Tilman et al. 2014). First, environmental factors may have stronger effects on stability and diversity-stability relationships due to broader abiotic gradients at larger spatial scales (Symstad et al. 2003, Hooper et al. 2005, Romanuk et al. 2009). Second, community composition varies temporally and spatially at large scales, in response to abiotic variation and multi-trophic interactions (Collins 2000, Ricklefs 2004), and the consequences for diversity-stability relationships are not certain (Tilman et al. 2014). As a result, the importance of diversity in determining stability is inconsistent across observational studies (e.g., Grman et al. 2010, Hallett et al. 2014) and in experiments where community composition is not maintained (Pfisterer et al. 2004, Bezemer and van der Putten 2007, Roscher et al. 2013), with some studies finding positive, negative or neutral diversity-stability relationships. In contrast, in experiments where richness is manipulated and composition is determined randomly, strong positive diversity-stability relationships are observed and relatively few species are needed to maximize stability (ca. 12 species; Tilman et al. 2006, Roscher et al. 2011). Against a backdrop of biotic and abiotic variation, it is hard to predict whether more or less diversity is required to support stability at large scales, or whether variation in diversity has consistent impacts on stability.

We evaluated the relative importance of richness, evenness, dominant species and environmental conditions for controlling three components of stability over three years in 28 grassland restorations. As severe drought conditions occurred in the second year of the study, we analyzed both *resistance* and *resilience* to drought, in addition to *temporal stability*. We asked 1) are species richness and evenness associated with stability? 2) How do diversity-stability relationships vary with the abundance of dominant species and across environments? And, 3) what is the relative importance of each putative driver of stability: diversity, dominant species abundances, and environmental factors?

Methods

Study sites

We sampled 28 grassland restorations across 1300 km^2 in southwest Michigan, USA during 2011-2013 (Grman et al. 2014). Between 2003 and 2008, former agricultural sites, ranging in size from 0.3 to 38.9 hectares (mean=5.3), were herbicided and seeded once with native tallgrass prairie grasses and forbs. Tallgrass prairie is commonly restored using these methods and, as a fire-dependent ecosystem, is managed with periodic prescribed fire to reduce woody species encroachment and promote native prairie species (Packard and Mutel 1997). Restored sites were sown with between 8 and 71 species (mean=35); observed richness was correlated with this gradient in seed mix richness (r=0.38, p=0.04). Averaged across all sites, sown species composed 42% of richness and 67% of cover. Non-sown species were both native and exotic in origin. Soils were primarily sandy loams or loams (USDA-NRCS 2014), but vary in physical (e.g, % sand) and chemical (e.g., nutrients) properties.

Drought

Southwest Michigan experienced a record heat wave and moderate to severe drought in summer 2012. Drought was most severe in July and early August, the peak growth period for tallgrass prairie plants (National Drought Mitigation Center et al. 2016). Mean temperature for June-August 2012 was 23.1 °C (8% above 1981-2010 normals), while precipitation ranged between 0.5 and 4 cm in June (5-25% of normals), and between 3 and 12 cm in July and August (25-75% of normals) (National Oceanic and Atmospheric Association 2016a,b).

Field sampling

We established 10 evenly spaced 1-m^2 plots along one 45 m transect in the center of each site. During peak productivity (July-September 2011), we harvested all live aboveground biomass from each 1-m^2 plot. We resampled each transect in October-November 2012 and September–October 2013, offsetting each successive transect by 5m to avoid previously harvested areas. Each year, we dried biomass for 72 hours at 65° C prior to weighing. In July-September 2011, prior to harvesting biomass, we recorded percent cover of all (sown and non-sown) vascular plant species in each 1-m^2 plot. All plants were identified to species when possible, and were otherwise included in diversity metrics only when they clearly represented unique taxa (Voss and Reznicek 2012).

Environmental factors

In grasslands, soil resources (moisture, nutrients) and natural disturbance regimes (primarily fire) affect diversity and productivity (Collins 2000, Knapp and Seastedt 1986, Baer et al. 2003), and are likely to influence diversity-stability relationships during drought

(Dimitrakopoulos et al. 2006, Koerner and Collins 2014). For example, soil fertility and moisture may disrupt or strengthen diversity-stability relationships (Hautier et al. 2014, Xu et al. 2015, Zhang et al. 2016), or increase or decrease stability directly without altering diversity-stability relationships (Leps 2004, Grman et al. 2010, Yang et al. 2012). We collected eight 20 × 3 cm^2 soil cores at each 1-m^2 plot in 2011 and analyzed pooled samples from each site for soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, and pH (Brookside Laboratories, New Knoxville, OH, USA). To assess the capacity of soil to retain moisture and alleviate drought impacts, we calculated the proportion of oven dried soil weight to saturated wet weight at the plot level (hereafter, soil water holding capacity; Brudvig and Damschen 2011) and used site means for analysis. To simplify site-level soils data, we conducted a principal components analysis. The first PCA axis (hereafter, soil PC1) explained 58% of the variance; higher values of soil PC1 represent sandier sites with lower water holding capacity and higher phosphorus. Land managers provided information on the history of prescribed fire at each site. We included two binomial indicator variables in our analysis: sites burned in 2011 (n=10) and 2013 (n=4). No burns occurred in 2012, the year of the drought. Finally, both productivity and the dependence of productivity on diversity increase over time in experiments (Tilman et al. 2012, Tilman et al. 2014). As stability and diversity-stability relationships may likewise be stronger in older restorations, we calculated the age (years since sowing) of each restoration in 2011.

Data analysis

Overview: To assess the relationship between diversity and stability (Question 1), we used multiple linear regressions testing whether richness and evenness were associated with each component of stability (temporal stability, resistance, and resilience). We used two different information-theoretic approaches to address Questions 2 and 3. Information-theoretic methods are ideal for evaluating evidence for multiple competing hypotheses, using observational data with limited replication (Stephens et al. 2005, Aho et al. 2014). First, we used model selection with AICc to assess whether diversity-stability relationships depend on the abundance of dominant species and environmental conditions (Question 2). Then, we performed model averaging to assess the relative importance of all predictors in determining stability (Question 3). All analyses were conducted using R 3.0.3 (R Core Team 2014).

Stability, diversity, and dominant species metrics: We calculated three measures of stability using the mean above-ground biomass/m^2 for each site in each year. Temporal stability, the inverse coefficient of variation in productivity over the years 2011-2013 (μ/σ), is a measure of the constancy of productivity over time. Resistance to drought {ln(biomass$_{2012}$/biomass$_{2011}$)} indicates the capacity to maintain productivity during drought conditions. Resilience to drought {ln(biomass$_{2013}$/biomass$_{2011}$)} indicates the capacity for recovery of productivity to pre-drought levels. For all stability metrics, higher values correspond with greater stability.

We partitioned diversity into richness and evenness. We calculated plot richness as the number of species observed and Simpson's evenness as E = $(1/\sum_{i=1}^{S} p_i^2\ ) \times 1/\mathrm{S}$, where p_i is the relative abundance of each 1 to S species, then averaged across plots within a site. Richness ranged from 3.7-28.2 species/m^2, and evenness from 0.15-0.38.

We classified dominant species as species with the highest percent cover in at least three sites. Species meeting these criteria are therefore common enough to be important in our system, and if they are particularly stable species, may contribute strongly to stability in sites where they are abundant. Three sown C_4 grasses (*Andropogon gerardii*, *Schizachyrium scoparium*, and *Sorghastrum nutans*), one non-sown exotic C_3 grass (*Poa pratensis*), and one non-sown native clonal forb (*Solidago canadensis*) were dominant in at least three sites, although abundances of these species varied considerably in abundance across all sites (Table S2.1). These five species also had the highest mean cover across sites. Because evenness also varied across sites, these species ranged in abundance between 14.1% and 53.3% in sites they dominated.

Question 1 - Diversity-stability relationships: We performed linear regressions to test whether diversity predicted each measure of stability, including both richness and evenness as independent variables. We also evaluated whether diversity-stability relationships were non-linear (by adding quadratic terms and performing likelihood ratio tests), but they were never significant (LRT, $\chi^2_{df=1\ or\ 2}$, all $p>0.10$). We used partial-R^2 to assess the relative importance of richness and evenness.

Question 2 - Effects of dominant species abundances and environmental factors on diversity-stability relationships: We used model selection to examine whether the effect of diversity on each stability metric varied by 1) dominant species abundances or 2) environmental factors (soilPC1, site age, 2011 burn, 2013 burn). For each stability metric, we built separate model sets for dominant species and environmental factors. Each model set included four types of simple models. We used a regression model testing the effect of richness and evenness on stability (first type; “diversity model”). We also used regression models adding a single environmental factor or dominant species to the diversity model, either with interactions with richness or evenness (second type; “interaction model”) or without interactions (third type; “nested additive model”).

As a baseline of no effect, we included a model with only an intercept term (fourth type; "intercept-only model"). This approach allowed us to simultaneously evaluate support for each "interaction hypothesis" that the effect of diversity on stability depends on each environmental driver or dominant species. By including nested additive models, we compared support for interaction hypotheses to more parsimonious "additive hypotheses" that each dominant species or environmental factor independently effects stability without influencing diversity-stability relationships.

We performed model selection with AICc, Aikake's information criterion corrected for small sample size (Burnham and Anderson 2002), with the ICtab function in the bbmle package (Bolker and R Core Team 2014). To assess support for each model within each set, we calculated the difference in AICc relative to the top-ranked model (ΔAICc) and Aikake weights (w_i). Aikake weights indicate model uncertainty, or the relative likelihood that each model is the best-fitting model, given the data and the set of models under consideration. Among models with good to moderate support overall ($\Delta\text{AICc} \leq 7$), 'competitive' models were those that fit as well or better than ($\Delta\text{AICc} \leq 2$) all models in which they were nested. Therefore, interaction models were only competitive when they fit better than nested additive, diversity, and intercept-only models. Models that fit poorly relative to the intercept-only model predicted no variation in stability. Interaction models that fit poorly relative to the diversity or nested additive models indicate insufficient evidence for an interactive effect, relative to the main effects of richness, evenness, environmental factors, or dominant species abundances. For all competitive interaction models, we examined the form of interactions graphically and calculated partial-R^2 to assess the relative importance of interactive and main effects. We also compared the log-likelihood of competitive interaction and nested additive models to rule out models with 'uninformative' interaction terms

(Arnold 2010). We standardized all continuous dependent variables to μ=0 and σ=0.5, the standard deviation for balanced binary predictors (Gelman 2008, Schielzeth 2010). Effect size of 2011 burns (10 of 28 sites, $\sigma = 0.49$) was therefore in the same scale as continuous predictors. Because 2013 burns were considerably less balanced (4 of 28 sites, $\sigma = 0.36$), estimates were biased slightly upwards.

Question 3 - Relative importance of diversity compared to other putative drivers for stability: We used model-averaged parameter estimates and relative importance values to compare the strength and magnitude of richness and evenness effects on stability to the effects of each dominant species and each environmental factor. Model-averaged parameter estimates ($\bar{\hat{\theta}}_i$) are calculated as the sum of estimates from each model i in a model set containing that predictor, weighted by each model's Aikake weight ($\sum w_i\, \hat{\theta}_i$) ('natural average' method; Burnham and Anderson 2002). When using standardized variables, model-averaging produces reliable estimates of the relative effect size of each predictor (Grueber et al. 2011). Relative importance values ($w_{+j} = \sum_{i\ for\ x_j} w_i$, where j=all models containing predictor x) indicate the importance of each predictor in determining the response on a scale of 0 (predictor in no models) to 1 (predictor in all models).

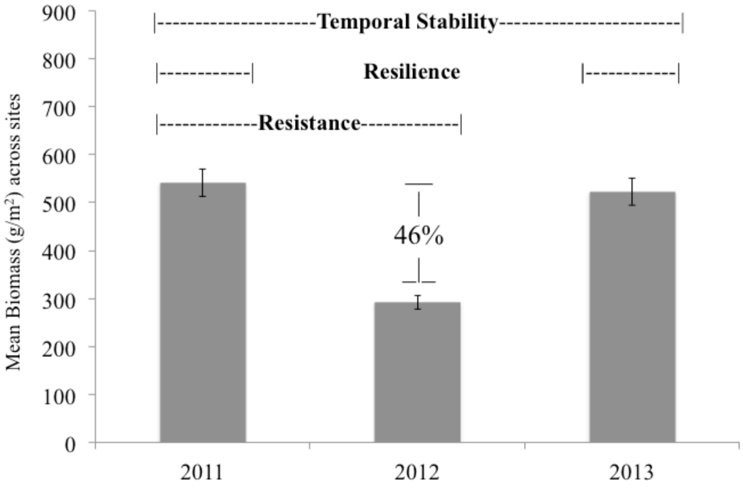
We conducted model-averaging with the 'dredge' and 'model.avg' functions in the MuMIn R library (Barton 2014). We generated a set of all possible models for each component of stability, including up to four terms to avoid overfitting models, and calculated ΔAICc and w_i for each model. Variance inflation factors for all three global models (containing all diversity, dominant species and environmental variables) were <6, and variables were generally not strongly correlated (Table S2.2). We did not include interaction models, which can bias both model-averaged estimates and importance values (Galipaud et al. 2014), and because evidence for the importance of interactions was weak (*see Results*). In large model sets, estimates from models with low weights may be spurious, so we restricted further analysis to all models with ΔAICc ≤ 4 (Burnham and Anderson 2002). For each predictor retained in each restricted model set, we calculated $\bar{\bar{\theta}}_i$, unconditional error estimates, and w_{+j} (Grueber et al. 2011) and compared the effect size of predictors where 90% unconditional confidence intervals did not include zero. We used 90% confidence intervals to avoid rejecting potentially important drivers, especially given the relatively small sample size (Arnold 2010).

Results

Drought effects on annual productivity

The 2012 drought reduced productivity by 46% (range: 22%-67%) between 2011 and 2012 (t_{27}= -11.36, p < 0.001) (Figure 2.1). Productivity returned to 96% (range: 46-179%) of pre-drought levels in 2013 (t_{27} = -0.67, p = 0.51).

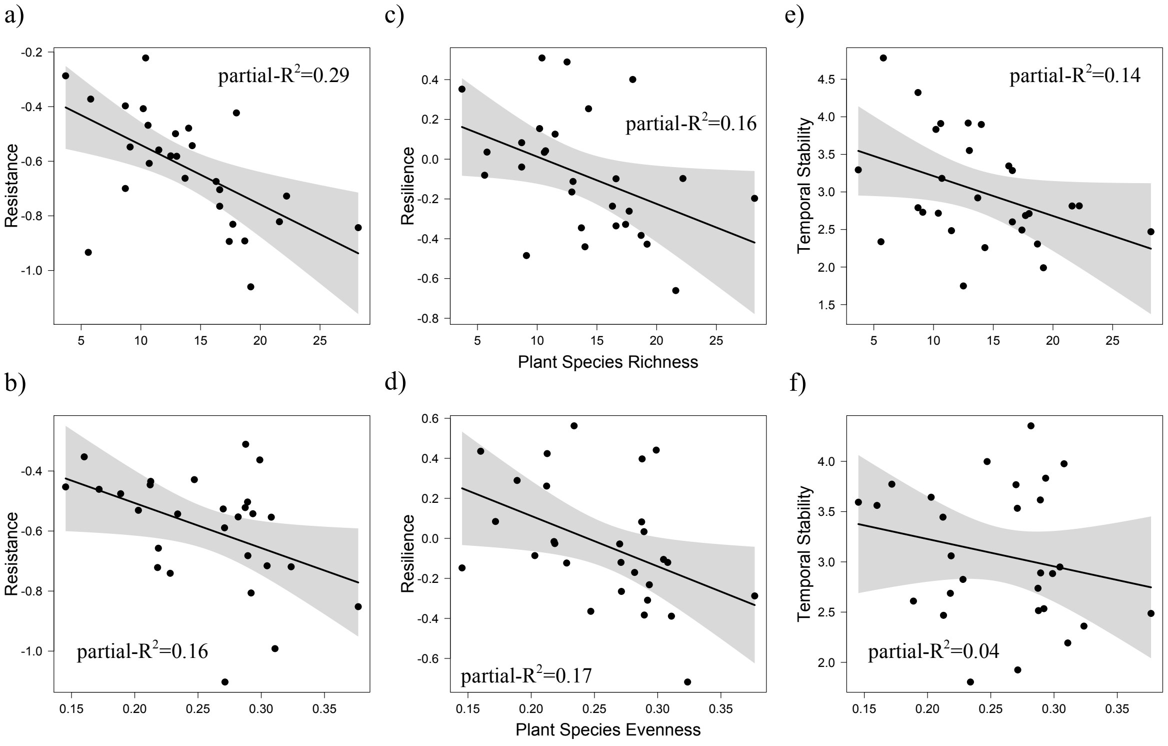
Figure 2.1. Across-site mean biomass (+ SE) in 2011, 2012, and 2013.



Question 1 - Diversity-stability relationships

Contrary to predictions, stability was higher in low diversity sites. Both richness and evenness were strongly associated with lower resistance (model adj-$R^2 = 0.25$) and resilience (model adj-$R^2 = 0.15$) to drought (Figure 2.2). Richness (but not evenness) was weakly associated with lower temporal stability (model adj-$R^2 = 0.07$) (Figure 2.2).

Figure 2.2. Effect of two components of diversity (richness and evenness) on three metrics of stability. Both plant species richness and evenness predict lower resistance (model $R^2 = 0.25$) (a,b) and resilience (model $R^2 = 0.15$) (c,d). Richness also predicts lower temporal stability (e), which is not correlated with evenness (f) (model $R^2 = 0.07$). Component residual plots showing effect of richness controlling for effect of evenness, and vice versa.



Question 2 - Effects of dominant species abundances and environmental factors on diversity-stability relationships

There was only weak evidence that diversity-stability relationships varied with dominant species abundances or the timing of prescribed fire. At least one interaction model occurred in most sets of competitive models (Tables 2.1, 2.2). However, competitive interaction models predicted stability no better than (within 2 AICc) diversity or nested additive models, and either interaction terms explained little variation in stability (small partial-R^2) or support for interaction

Table 2.1. **Model selection results of environmental interaction, nested additive, and diversity models (dAICc ≤ 4.0) for a) resistance, b) resilience, and c) temporal stability.** Competitive models **in bold**. Env=Environmental factor. Standardized effect size shown for each predictor in model (**p<0.01, *p<0.05, +p<0.10), with partial-R^2 in parentheses. Terms not in model indicated with a dash (-). For each model: logLik=log-likelihood, dAICc=delta AICc.

a) Resistance

Model type	**Factor**	**Richness**	**Evenness**	**Env**	**Env*R**	**Env*E**
diversity	**-**	**-0.24** (0.29)**	**-0.16* (0.16)**	**-**	**-**	**-**
nested additive	soilPC1	-0.24** (0.29)	-0.17* (0.16)	-0.03 (0.01)	-	-
nested additive	burn2011	-0.22* (0.18)	-0.16+ (0.15)	-0.03 (0.01)	-	-
nested additive	age	-0.24** (0.25)	-0.16* (0.16)	0.00 (0.00)	-	-

b) Resilience

Model type	**Factor**	**Richness**	**Evenness**	**Env**	**Env*R**	**Env*E**
interaction	**burn2013**	**-0.32** (0.27)**	**-0.12 (0.21)**	**-0.23** (0.26)**	**-**	**-0.09**
nested additive	**burn2013**	**-0.36** (0.28)**	**-0.25* (0.19)**	**0.40* (0.24)**	**-**	**-**
nested additive	**soilPC1**	**-0.28* (0.20)**	**-0.28* (0.20)**	**-0.22* (0.16)**	**-**	**-**
interaction	burn2013	-0.26* (0.18)	-0.26* (0.18)	-0.20* (0.24)	0.01 (0.00)	-

c) Temporal Stability

Model type	**Factor**	**Richness**	**Evenness**	**Env**	**Env*R**	**Env*E**
intercept	**-**	**-**	**-**	**-**	**-**	**-**
interaction	**burn2011**	**-0.27 (0.03)**	**-0.03 (0.03)**	**0.25 (0.10)**	**-**	**0.53+ (0.15)**
diversity	**-**	**-0.59+ (0.14)**	**-0.30 (0.04)**	**-**	**-**	**-**
nested additive	**burn2011**	**-0.27 (0.02)**	**-0.23 (0.03)**	**-0.51 (0.09)**	**-**	**-**
interaction	burn2011	-0.20 (0.02)	-0.15 (0.01)	0.31+ (0.09)	-0.40 (0.06)	-
nested additive	soilPC1	-0.58+ (0.13)	-0.29 (0.04)	0.19 (0.02)	-	-
nested additive	age	-0.51 (0.09)	-0.29 (0.04)	0.15 (0.01)	-	-

Table 2.1. (cont'd)

a) Resistance

Model type	**Factor**	**logLik**	**dAICc**	**df**	**weight**	**R^2**
diversity	**-**	**10.5**	**0**	**4**	**0.46**	**0.25**
nested additive	soilPC1	10.6	2.7	5	0.12	0.22
nested additive	burn2011	10.6	2.8	5	0.12	0.22
nested additive	age	10.5	3	5	0.1	0.22

b) Resilience

Model type	**Factor**	**logLik**	**dAICc**	**df**	**weight**	**R^2**
interaction	**burn2013**	**2.6**	**0**	**6**	**0.39**	**0.38**
nested additive	**burn2013**	**0.8**	**0.3**	**5**	**0.33**	**0.32**
nested additive	**soilPC1**	**-0.5**	**2.9**	**5**	**0.09**	**0.26**
interaction	burn2013	0.8	3.6	6	0.07	0.3

c) Temporal Stability

Model type	**Factor**	**logLik**	**dAICc**	**df**	**weight**	**R^2**
intercept	**-**	**-29.8**	**0**	**2**	**0.26**	**0**
interaction	**burn2011**	**-24.2**	**0.3**	**6**	**0.22**	**0.21**
diversity	**-**	**-27.7**	**1.1**	**4**	**0.15**	**0.07**
nested additive	**burn2011**	**-26.4**	**1.5**	**5**	**0.12**	**0.12**
interaction	burn2011	-25.5	3	6	0.06	0.13
nested additive	soilPC1	-27.4	3.5	5	0.04	0.05
nested additive	age	-27.6	3.8	5	0.04	0.04

models was similar to the intercept-only model (Table 2.1, 2.2). This suggests that, even among competitive interaction models, interactions were weak overall (Figure S2.1), and never more important than the main effects of diversity, environmental factors, and dominant species.

Question 3 - Relative importance of diversity compared to other putative drivers for stability

Diversity and environmental factors (especially prescribed fire) were important predictors of stability, while dominant species played a more limited role (Table 2.3). Effects on temporal stability were weak overall, while several factors predicted both resistance and resilience well. To compare the effect size of putative stability drivers, we present only model-averaged parameter estimates here ($\bar{\bar{\theta}}_i$); see Table 2.3 for full summary of statistics, including unconditional error estimates and relative importance values. Greater abundances of *S.*

canadensis reduced resistance ($\bar{\hat{\theta}}_i$ = -0.14) (Figure S2.2a), but it did so more weakly than richness (-0.26) and evenness (-0.17) (Table 2.3). Richness (-0.35) and evenness (-0.26) were also strongly associated with lower resilience to drought, when compared to sites where soil is

Table 2.2. Model selection results of dominant species interaction, nested additive, and diversity models (dAICc ≤ 4.0) for a) resistance, b) resilience, and c) temporal stability. Competitive models **in bold**. Dom=Dominant species. Standardized effect size shown for each predictor in model (**p<0.01, *p<0.05, +p<0.10), with partial-R^2 in parentheses. Terms not in model indicated with a dash (-). For each model: logLik=log-likelihood, dAICc=delta AICc. Andger = *Andropogon gerardii*, Poapra = *Poa pratensis*, Schsco = *Schizachyrium scoparium*, Solcan = *Solidago canadensis*, Sornut = *Sorghastrum nutans*.

a) Resistance

Model type	Factor	Richness	Evenness	Dom	Dom*R	Dom*E
nested additive	**Solcan**	**-0.27*** (0.37)**	**-0.17* (0.21)**	**-0.15* (0.18)**	**-**	**-**
interaction	**Solcan**	**-0.26** (0.39)**	**-0.20* (0.26)**	**-0.14* (0.20)**	**0.22 (0.08)**	**-**
diversity	**-**	**-0.24** (0.29)**	**-0.16* (0.16)**	**-**	**-**	**-**
interaction	Solcan	-0.27** (0.34)	-0.17* (0.21)	-0.15* (0.18)	-	0.01 (0.00)

b) Resilience

Model type	Factor	Richness	Evenness	Dom	Dom*R	Dom*E
diversity	**-**	**-0.26* (0.16)**	**-0.28* (0.17)**	**-**	**-**	**-**
intercept-only	**-**	**-**	**-**	**-**	**-**	**-**
nested additive	Schsco	-0.26* (0.15)	-0.29* (0.18)	-0.07 (0.02)	-	-
nested additive	Sornut	-0.30* (0.16)	-0.27* (0.17)	0.08 (0.01)	-	-
nested additive	Andger	-0.29* (0.16)	-0.28* (0.17)	-0.06 (0.01)	-	-
nested additive	Solcan	-0.27* (0.16)	-0.28* (0.17)	-0.03 (0.00)	-	-
nested additive	Poapra	-0.26* (0.15)	-0.28* (0.17)	0.00 (0.00)	-	-

c) Temporal Stability

Model type	Factor	Richness	Evenness	Dom	Dom*R	Dom*E
nested additive	**Schsco**	**-0.55+ (0.14)**	**-0.40 (0.08)**	**-0.53+ (0.15)**	**-**	**-**
intercept-only	**-**	**-**	**-**	**-**	**-**	**-**
diversity	**-**	**-0.59+ (0.14)**	**-0.30 (0.04)**	**-**	**-**	**-**
interaction	**Schsco**	**-0.55+ (0.15)**	**-0.38 (0.08)**	**-0.60* (0.16)**	**-**	**-0.52 (0.05)**
interaction	**Schsco**	**-0.43 (0.14)**	**-0.32 (0.05)**	**-0.53* (0.16)**	**0.62 (0.05)**	**-**
nested additive	Solcan	-0.65* (0.17)	-0.32 (0.05)	-0.39 (0.08)	-	-
nested additive	Sornut	-0.79* (0.18)	-0.27 (0.03)	0.36 (0.05)	-	-
nested additive	Andger	-0.46 (0.07)	-0.29 (0.04)	0.25 (0.03)	-	-
interaction	Solcan	-0.62* (0.18)	-0.41 (0.08)	-0.37 (0.09)	-0.71 (0.05)	-

Table 2.2. (cont'd)

a) Resistance

Model type	**Factor**	**logLik**	**dAICc**	**df**	**weight**	**R^2**
nested additive	**Solcan**	**13.3**	**0**	**5**	**0.40**	**0.36**
interaction	**Solcan**	**14.5**	**1**	**6**	**0.25**	**0.38**
diversity	**-**	**10.5**	**2.7**	**4**	**0.11**	**0.25**
interaction	Solcan	13.3	3.3	6	0.08	0.33

b) Resilience

Model type	**Factor**	**logLik**	**dAICc**	**df**	**weight**	**R^2**
diversity	**-**	**-3**	**0**	**4**	**0.28**	**0.15**
intercept-only	**-**	**-6.3**	**1.5**	**2**	**0.14**	**0**
nested additive	Schsco	-2.7	2.6	5	0.08	0.13
nested additive	Sornut	-2.8	2.6	5	0.08	0.13
nested additive	Andger	-2.8	2.7	5	0.07	0.12
nested additive	Solcan	-2.9	2.9	5	0.07	0.12
nested additive	Poapra	-3	3	5	0.06	0.12

c) Temporal Stability

Model type	**Factor**	**logLik**	**dAICc**	**df**	**weight**	**R^2**
nested additive	**Schsco**	**-25.4**	**0**	**5**	**0.23**	**0.18**
intercept-only	**-**	**-29.8**	**0.4**	**2**	**0.19**	**0**
diversity	**-**	**-27.7**	**1.6**	**4**	**0.11**	**0.07**
interaction	**Schsco**	**-24.7**	**1.8**	**6**	**0.10**	**0.18**
interaction	**Schsco**	**-24.8**	**1.9**	**6**	**0.09**	**0.18**
nested additive	Solcan	-26.5	2.1	5	0.08	0.11
nested additive	Sornut	-27	3.2	5	0.05	0.08
nested additive	Andger	-27.3	3.8	5	0.03	0.05
interaction	Solcan	-25.8	4	6	0.03	0.11

sandy with low water holding capacity (-0.22) (Figure 2.3), and the abundance of *A. gerardii* is high (-0.21) (Figure S2.2b) (Table 3). Sites burned in 2013 were more resilient (0.40) (Figure 2.4a), but this effect size may be biased upward, as only 4 sites were burned in 2013. Temporal stability was lower in sites burned in 2011 (-0.66) (Figure 2.4b). 2011 burns reduced temporal stability more strongly than *Schizachyrium scoparium* abundance (-0.54) (Figure 2.S2c, Table

2.3). Richness and evenness did not strongly predict temporal stability when controlling for other factors.

Table 2.3. Results of model averaging from confidence sets (all models ΔAICc ≤ 4) for each measure of stability. Model-averaged estimate ($\bar{\bar{\theta}}_i$), unconditional (adjusted) SE, 90% CI, and relative importance value (Imp) shown for all predictors retained in each confidence set. Values in **bold** indicate estimates where 90% CI did not include zero; predictors in **bold** are important for at least one stability metric. Effects of 2013 burns (Burned 2013) on resistance not modeled; *S. scoparium*, *S. nutans*, *P. pratensis*, *S. canadensis*, Burned 2011, and Restoration age not retained as predictors in confidence set for resilience.

	Resistance				*Resilience*				*Temporal Stability*			
	$\bar{\bar{\theta}}_i$	SE	(90% CI)	Imp	$\bar{\bar{\theta}}_i$	SE	(90% CI)	Imp	$\bar{\bar{\theta}}_i$	SE	(90% CI)	Imp
Diversity												
Richness	**-0.26**	**0.08**	**(-0.39, -0.13)**	**1.00**	**-0.35**	**0.11**	**(-0.54, -0.17)**	**1.00**	-0.43	0.33	(-0.96, 0.11)	0.26
Evenness	**-0.17**	**0.08**	**(-0.30, -0.05)**	**0.94**	**-0.26**	**0.11**	**(-0.43, -0.09)**	**0.88**	-0.28	0.32	(-0.80, 0.24)	0.11
Dominant spp.												
A. gerardii	0.00	0.02	(-0.16, 0.10)	0.07	**-0.21**	**0.12**	**(-0.41, -0.01)**	**0.12**	0.25	0.31	(-0.26, 0.76)	0.08
S. scoparium	-0.01	0.03	(-0.17, 0.05)	0.11	-	-	-	-	**-0.54**	**0.32**	**(-1.07, -0.02)**	**0.46**
S. nutans	0.00	0.02	(-0.18, 0.11)	0.07	-	-	-	-	0.54	0.39	(-0.09, 1.17)	0.27
P. pratensis	0.00	0.02	(-0.13, 0.09)	0.07	-	-	-	-	0.01	0.28	(-0.44, 0.46)	0.04
S. canadensis	**-0.14**	**0.08**	**(-0.26, -0.04)**	**0.91**	-	-	-	-	-0.34	0.28	(-0.79, 0.11)	0.22
Env. Factors												
Soil PC1	0.00	0.03	(-0.16, 0.06)	0.09	**-0.22**	**0.10**	**(-0.39, -0.07)**	**0.86**	0.40	0.29	(-0.08, 0.87)	0.31
Burned 2011	0.00	0.02	(-0.15, 0.13)	0.06	-	-	-	-	**-0.66**	**0.34**	**(-1.22, -0.10)**	**0.59**
Burned 2013	-	-	-	-	**0.40**	**0.14**	**(0.17, 0.64)**	**1.00**	-0.05	0.46	(-0.80, 0.70)	0.04
Restoration age	0.00	0.02	(-0.12, 0.13)	0.06	-	-	-	-	0.39	0.41	(-0.27, 1.05)	0.13

Figure 2.3. Effect of soil moisture and texture (soil PC1) on drought resilience. Sites with higher clay and water holding capacity (WHC) are more resilient. Residual plot controlling for effects of other variables identified as important from model averaging (*see Table 3.3*).

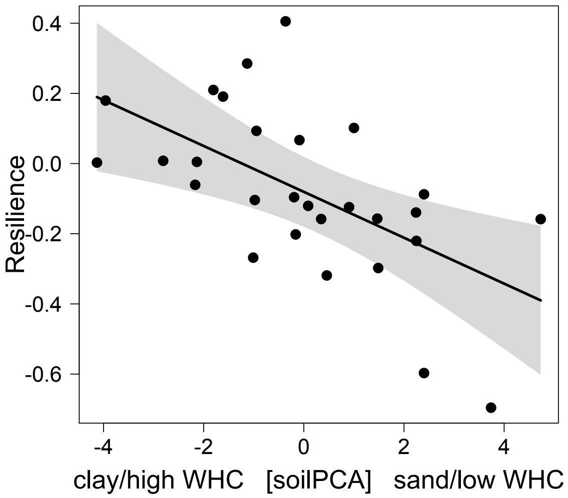
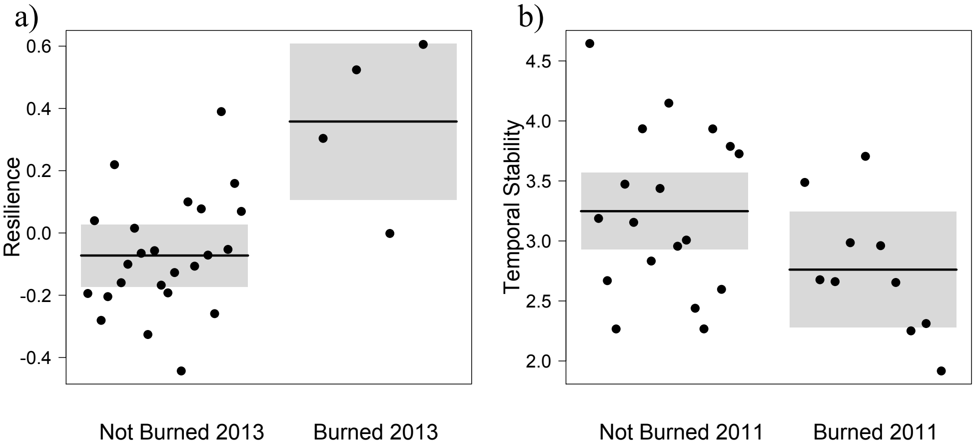


Figure 2.4. Timing of prescribed fire impacts stability. a) Post-drought fire supports resilience while b) pre-drought fire reduces temporal stability. Residual plots controlling for effects of other variables identified as important from model averaging (*see Table 2.3*).



Discussion

Theory (Yachi and Loreau 1999, Lehman and Tilman 2000) and experiments (Gross et al. 2014, Isbell et al. 2015) demonstrate that diversity can stabilize community productivity, but the importance of diversity relative to biotic and abiotic environmental variation at the scale of natural communities is poorly understood (Cardinale 2012, Tilman et al. 2014). Here, we analyzed the relationship between plant species diversity and stability in 28 grassland restorations, revealing two important findings. First, both components of diversity, richness and evenness, were strongly associated with lower resistance and resilience to drought, and richness was weakly associated with lower temporal stability. Second, the negative effects of richness and evenness on resistance and resilience were at least as strong as environmental factors and dominant species abundances. The most stable sites had lower species richness and evenness, were burned after and not before drought; had soils high in clay and moisture retention capacity, but low in phosphorus; and tended to have low abundances of some dominant species (*Andropogon gerardii*, *Schizachyrium scoparium*, *Solidago canadensis*).

Diverse sites were less stable

What distinguishes our system, where stability was lower in diverse sites, from the majority of studies that find positive diversity-stability relationships? Diversity may be more likely to reduce stability: 1) in certain communities or under certain perturbations, such as grassland plant communities under drought, 2) in certain community structures (i.e., composition), 3) when community composition is free to vary through natural colonization and extinction dynamics, particularly during early succession, or 4) under certain environmental conditions. We discuss each of these hypotheses below.

First, studies of other grassland plant communities have detected negative diversity-stability relationships in response to drought (Pfisterer and Schmid 2002, Van Peer et al. 2004, van Ruijven and Berendse 2010, Vogel et al. 2012). However, diversity in algal and microbial communities has also been associated with reduced stability (Petchey et al. 2002, Allison 2004, Gonzalez and Descamps-Julien 2004, Zhang and Zhang 2006), so negative relationships are not unique to grassland plant communities. Furthermore, negative diversity-stability relationships occur in the same community types, across similar richness gradients, and in response to the same perturbations where positive and neutral relationships are more frequently observed (Griffin et al. 2009). Therefore, it seems unlikely that negative diversity-stability relationships are a distinctive property of grasslands plant communities under drought.

Second, variation in community composition, rather than diversity per se, may drive stability. Other grassland studies show that the stability of dominant species often determines community stability (Smith et al. 2004, Polley et al. 2007). Low diversity sites in our system may be more stable because a large proportion of biomass in these sites is composed of stable dominant species that are less abundant in high diversity sites. A single dominant species, *Andropogon gerardii,* was more abundant in low-richness sites, while other dominant species were either less abundant or not correlated with richness (Table S2.2, S2.4). Regardless, if particular dominant species contribute disproportionately to community stability, sites in which they are most abundant should be more stable. Instead, dominant species abundances were poor predictors of stability. The abundance of three dominant species, *A. gerardii*, *Schizachyrium scoparium*, and *Solidago canadensis*, was associated with lower stability. While *S. canadensis* is typically associated with drought-sensitivity (Hoover et al. 2014, Smith et al. 2016), the weak and negative effect among C_4 grasses (*A. gerardii*, *S. nutans*, *S. scoparium*) is surprising as they frequently support stability in both remnant and restored grasslands (e.g., Tilman and Downing 1994, Smith et al. 2004, Polley et al. 2007). Finally, when controlling for the effects of dominance and dominant species abundances, species richness was still strongly associated with lower stability. Even in regression models where higher dominance (low evenness) predicted greater stability, the independent negative effect of richness was at least as strong as the effect of evenness in the same models. Controlling for other components of dominance also did not alter how richness and evenness influenced stability (Table S2.3).

Third, communities experiencing successional changes may respond differently to perturbations than communities that are closer to equilibrium. The way composition changes through time, via colonization and extinction of both sown and non-sown species, may alter diversity-stability relationships. Diversity-stability relationships are typically weak in grassland experiments allowing natural colonization, compared to plots where composition is maintained (Pfisterer et al. 2004, Bezemer and van der Putten 2007, Roscher et al. 2013). Composition, as well as diversity and abundance, shifts in grassland restorations over at least the first decade of establishment (Sluis 2002, Heslinga and Grese 2010, Grman et al. 2013). In young (9 and 20 yr) grassland restorations in Texas, stability was negatively correlated with species richness as in our study, and not correlated with richness in nearby remnant grasslands (Polley et al. 2007). Additionally, root systems and soil microbial communities likely mediate aboveground drought responses and may be poorly developed in young communities restored in former agricultural land (Antoninka et al. 2009, Bauer et al. 2015).

Diversity effects on resistance and resilience were strong relative to environmental drivers

Although negatively correlated, diversity was a strong predictor of stability in our system, relative to putative environmental drivers. Notably, diversity was the strongest predictor of resistance and resilience, even when controlling for covariation between diversity and several factors known to drive both diversity and stability in grasslands. Only one environmental driver (fire) in our study was stronger than diversity for one measure of stability (temporal stability), although neither diversity nor fire predicted temporal stability well. Experimental manipulations of precipitation (Xu et al. 2014), disturbance (mowing; Vogel et al. 2012) and fertilization (Hautier et al. 2014, Xu et al. 2015), on the other hand, frequently weaken or overwhelm diversity-stability relationships (but see Tilman et al. 2006, Xu et al. 2014). Experimental treatments (nitrogen and water addition, mowing) likely have stronger effects because they are applied at much greater levels than the analogous environmental effects we modeled (soil nutrients and water holding capacity, and prescribed fire), and vary independently of other biotic and abiotic conditions. Our results contrasted with experimental results in other ways, as well, particularly how the importance of diversity and abiotic treatments vary across components of stability. In experiments, both are likely to drive temporal stability and resistance, but not resilience (e.g., Tilman et al. 2006, Isbell et al. 2015). Diversity in our system, in contrast, had particularly strong (negative) effects on both resistance and resilience, but not temporal stability. Environmental drivers were linked to temporal stability and resilience, but not resistance. Diversity-stability relationships were also never negative in experiments explicitly comparing diversity and environmental factors. When diversity is destabilizing, as in our system, it may have stronger impacts on both resistance and resilience than other drivers. Therefore, the relative importance of diversity and environmental factors likely depends on both the direction of diversity effects and the intensity of environmental gradients.

The timing of fire, and to a lesser extent the influence of soil properties, had important consequences for stability. Pre-drought fire reduced temporal stability, while post-drought fire supported resilience. Pre-drought fires may have increased drought susceptibility by stimulating a pulse in productivity and reducing soil resources (Blair 1997, Turner et al. 1997, Craine and Nippert 2014). This suggests, however, that sites burned in 2011 should also be less resistant and possibly less resilient, which we did not find. Moisture and texture defined the strongest gradients in soil resources (soil PC1). Unsurprisingly, less sandy sites with greater soil water holding capacity were better able to rebound from drought. Sites burned in 2013, in contrast, rebounded strongly. Together, this suggests that stability was driven in part by the fact that fire stimulated productivity in non-drought years, but productivity at all sites was limited by water holding capacity during drought.

Conclusions

In contrast to the extensive experimental evidence that plant species richness stabilizes community productivity (Gross et al. 2014, Isbell et al. 2015), we found that both plant species richness and evenness in grassland restorations was associated with lower stability. This negative association of diversity with resistance and resilience to drought was 1.2-1.9 times stronger than other putative stability drivers, including prescribed fire, soil properties, site age, and dominant species' abundance. Diversity-stability relationships vary widely at large scales, ranging from weakly negative to strongly positive in both naturally-assembled plant communities (e.g., Grman et al. 2010, Hallett et al. 2014) and other grassland restorations (Biondini 2007, Polley et al.

2007, Carter and Blair 2012), likely because a complex suite of biotic and abiotic factors drive temporal and spatial variation in diversity-stability relationships. Better predictions of when large-scale diversity-stability relationships are positive vs. negative or neutral, will likely require large-scale experiments that replicate species diversity manipulations across realistic environmental gradients.

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APPENDIX

Table S2.1. Percent cover of most abundant species. Species dominant at site in **bold**. Andger = *Andropogon gerardii*, Broine = *Bromus inermis*, Hiespp = *Hieracium species*, Junten = *Juncus tenuis*, Monfis = *Monarda fistulosa*, Panvir = *Panicum virgatum*, Poapra = *Poa pratensis*, Rubocc = *Rubus occidentalis*, Schsco = *Schizachyrium scoparium*, Solcan = *Solidago canadensis*, Solspe = *Solidago speciosa*, Sornut = *Sorghastrum nutans*, Tripra = *Trifolium pratense*.

site	*Andger*	*Broine*	*Hiespp*	*Junten*	*Monfis*	*Panvir*	*Poapra*	*Schsco*	*Solcan*	*Solspe*	*Sornut*	*Tripra*
1	**37.5**	0	0	0	0	0	3	0.3	0	0	10.6	0
2	**29**	0	0	0	0	0	0	3.25	3.1	0	0.73	0
3	7.7	0.04	0.01	0.04	0	1.41	0.08	**27.9**	5.78	0	6.24	0
4	4.6	0	0	0.23	0	0.31	0.02	11.3	**30.5**	0	10.2	0
5	8.9	0.2	0	0.77	3.2	3.15	11.9	0.2	0.1	0	**41.5**	2.26
6	**39**	0	0	0	6.7	2.6	0	7	0.1	0	10.7	0
7	10.4	0	0	0.01	0.2	1.15	2.05	7.81	0.4	0	**28.5**	3.06
8	17	0	0	**17.2**	3.8	0	14	8.2	5.6	0.2	4.1	0
9	21.6	0	0.03	0.3	2.95	0	**38.5**	7.3	1.38	0.2	4.6	0.07
10	2.5	1.25	0	0	4.04	0.2	0	**27.5**	1.2	0	12.7	0
11	**33**	0	0	0	3.3	2.7	7.32	5.35	0	0	3.72	0
12	**18.3**	0	0	0.45	0.141	0.65	0	4.74	0	0	16	0
13	11.1	0	0.08	0	0.12	**16.83**	0.13	0	11.5	0	4	0
14	25.8	0	0	0	0.46	2.6	**34.5**	2.46	0	0	12.6	0.01
15	3	2.55	0.1	0	0.9	0.05	**53.3**	8.5	23.7	0	0.33	0.01
16	1	5.6	0	0	4.6	0	**31.3**	2	10.9	0.33	8	0.01
17	2.7	0.02	0	4.8	0.03	0.4	2.2	12.7	0.2	0.6	**46**	0
18	8	0	0	0	0	0	2.65	**30.5**	3.04	0	5.3	0
19	3.2	0	0	5.07	0	0	0.03	8.25	4.9	14.5	**15.3**	0
20	0	0	0	0	1.35	0.4	4.7	8.5	0	0	5.3	**33.5**
21	**45**	0	0	0	0.4	0.05	0	2.82	14.3	0	3.04	0
22	10.2	0	**29.5**	0	0	0.1	0.03	8.1	0.04	0	16.6	0
23	**25.2**	0	0	0	2.05	0.2	0.1	0.2	15.24	0	1.75	0
24	7.8	14	0	0	3.64	0.9	6.4	3.2	**14.2**	0	8.5	0
25	4.7	0.07	0	0	2.6	0.5	21.3	**36**	3	0	4.2	0
26	13.7	0	0	0.1	3.78	1.4	0	9.3	0.42	2.8	**25**	0
27	**14.1**	0	0	0	3.98	0.001	0	2.87	0.5	0	2	0
28	16.6	0	0	0	13.92	0.011	0	3.56	**16.8**	0	1.7	0
# sites dominant	8	0	1	1	0	1	4	4	3	0	5	1
mean % cover	15.06	0.85	1.06	1.03	2.22	1.27	8.34	8.92	5.96	0.67	11.04	1.39

Table S2.2. Pearson correlation coefficients between all predictors used in "global model" for model averaging. ***p < 0.001, **p < 0.01, *p < 0.05, +p < 0.10.

	Richness	Evenness	Soil PCA	Age	2011 Burn	2013 Burn	*Andger*	*Sornut*	*Schsco*	*Solcan*
Evenness	-0.44*									
Soil PCA	-0.03	-0.01								
Age	-0.45*	0.16	-0.07							
2011 Burn	0.59**	-0.15	0.04	-0.57**						
2013 Burn	0.33+	-0.21	-0.02	-0.45*	0.33+					
Andger	-0.49**	0.20	-0.27	0.47*	-0.48*	-0.05				
Sornut	0.57**	-0.31	0.01	-0.75***	0.53**	0.62***	-0.26			
Schsco	0.16	-0.23	0.37*	-0.15	0.45*	-0.08	-0.42*	-0.04		
Solcan	-0.15	0.01	-0.13	0.11	0.03	-0.24	-0.15	-0.37*	-0.12	
Poapra	-0.11	-0.08	-0.09	0.09	-0.20	-0.14	-0.15	-0.17	-0.02	0.16

CHAPTER THREE

MORE IS BETTER – SOWING MORE SPECIES AT HIGHER DENSITIES SUPPORTS GREATER NATIVE SPECIES RICHNESS IN PRAIRIE RESTORATIONS THAN PREDICTED BY NATIVE-EXOTIC RELATIONSHIP

Abstract

Given dramatic losses of native species due to human activities, the restoration of native biodiversity in degraded habitats is a primary aim of land managers. A major challenge to restoration is to design strategies that simultaneously benefit the establishment of native species and discourage the establishment of exotic species. A better understanding of positive correlations between native and exotic species richness, a pattern that is nearly ubiquitous at large scales in plant communities, may help managers modify these correlations to favor native plant species during restoration. Across 29 tallgrass prairies restored through seed sowing onto former agricultural lands, we examined: whether the relationship between native and exotic richness is 1) altered by management, such as seed additions and prescribed fire, 2) controlled instead by environmental conditions and successional processes, or 3) whether management is effective at altering native-exotic richness relationships in certain environments and limited in others. As is commonly found, native and exotic richness were positively correlated at large scales (e.g., across sites). However, management actions explained much of the remaining variation in native richness, while environmental conditions explained very little. Sites sown with more species at higher seeding rates, especially forb species, had higher native richness than predicted by the native-exotic relationship. In contrast, older sites had proportionally lower native richness, because native richness, and not exotic richness, declined with restoration age. We show that management actions, such as seed sowing, can modify the native-exotic richness

relationship to favor native species during restoration. The development of management actions that proportionally favor native species over time will further benefit native species restoration.

Introduction

Anthropogenic habitat degradation leads to native plant species loss (Vitousek et al. 1997, Foley et al. 2005, Rockstrom et al. 2009), so a primary goal of restoring habitats is to reassemble a diverse native community (Ruiz-Jaen and Aide 2005, Brudvig 2011). This goal is addressed directly (e.g., plant or seed additions), as well as indirectly through management actions designed to increase native diversity and resist invasion by exotic species (e.g., prescribed fire, carbon addition) (Suding 2011). Yet, efforts to restore native diversity are frequently limited by exotic species invasions (Didham et al. 2007, Matthews and Spyreas 2010, Kettenring and Adams 2011). Previously, we have compared a range of management and environmental factors to explain variation in both native and exotic species (see Chapter 4; Grman et al. 2013). Here, we address the challenge of simultaneously promoting native species and reducing exotic species in the context of native-exotic richness relationships (Fridley et al. 2007).

The correlation between native and exotic species richness has been well explored in both experimental systems and natural habitats, and provides a useful theoretical framework for understanding how the restoration of diverse native-dominated communities is connected to limiting exotic species invasions (Suding and Gross 2006, Fridley et al. 2007, Hill and Fischer 2014). Early theory predicted negative native-exotic richness relationships, because resources in diverse native communities should be more fully exploited, leaving less niche-space for exotic species to invade (Elton 1958, Levine et al. 2004). Therefore, restorations that increase native richness should also reduce exotic richness. Results from many small-scale observational and experimental communities support this theory and find that exotic richness is negatively correlated with native richness (e.g., Kennedy et al. 2002, Brown and Peet 2003. However, several decades of observations and experiments across a range of habitat types reveal that correlations can range from negative to positive to neutral, and are particularly variable at small scales (Fridley et al. 2007, Guo 2015).

At large scales, on the other hand, native and exotic richness correlations are consistently positive (Fridley et al. 2007). In other words, at scales most relevant to restoration, natural habitats with more native species also support more exotic species. Positive correlations between native and exotic species richness may result from similar responses of these groups to environmental gradients of increasing resource availability (Stohlgren et al. 1999, Davis et al. 2000) and increasing heterogeneity of resources (Davies et al. 2005, Melbourne et al. 2007), the frequency and intensity of disturbance (Taylor and Irwin 2004, Belote et al. 2008), and immigration rates (Tilman 1997). Given the range of potential causes, positive correlations may also result if native and exotic richness respond to different drivers operating simultaneously (Carboni et al. 2010, Parker et al. 2010, Jauni and Hyvonen 2012, Brummer et al. 2016). Native-exotic richness relationships may also strengthen or weaken over time, depending on whether competition-colonization tradeoffs or other successional processes lead to disproportionate losses of either native or exotic species (Tilman 1994, Molina-Montenegro 2012). Null modeling approaches also predict positive correlations at large scales, in the absence of these niche-based factors, if communities are assembled randomly from a regional species pool with a fixed ratio of native to exotic species (Fridley et al. 2004, Herben et al. 2004). Regardless of the mechanism, restoration of native richness at meaningfully large spatial scales may also facilitate or encourage increases in exotic richness.

A better understanding of native-exotic richness relationships may improve the ability of managers to design restoration strategies to proportionally favor native species. Importantly, if multiple drivers underlie positive native-exotic correlations but affect native and exotic species differently, managers may be able to identify which drivers more strongly support native species, but inhibit or minimally affect exotic species, and tailor their approaches accordingly. Here, we assess the relationship between native and exotic plant species richness in former agricultural land restored to tallgrass prairie grasslands through seed sowing. We also explore whether management and a range of environmental factors shift native-exotic richness relationships to favor native species.

Both seed addition and fire are considered critical for restoring native plant diversity in tallgrass prairie (Foster et al. 2007). Increases in native richness with seed additions indicate chronic seed limitation in this system (Carter and Blair 2012, Grman et al. 2013, Foster et al. 2015), due to the contemporary rarity of many tallgrass prairie species across their historical range (Samson and Knopf 1994). However, the effectiveness of native seed additions to restore species composition and diversity in prairies may still be limited, particularly under some abiotic conditions, for example those related to soil moisture and fertility (Foster et al. 2004, Myers and Harms 2011). The necessity of fire is indicated in part by the decline in plant species diversity in remnant prairie habitats over decadal time scales as a result of fire suppression (Leach and Givnish 1996, Alstad et al. 2016). However, whether burning increases or decreases native richness relative to exotic richness may depend on other factors, such as fire frequency and edaphic conditions (Howe 1994, Collins 2000, Howe 2011, Bowles and Jones 2013). Few studies have explicitly considered whether particular restoration actions like seed sowing and fire can increase native richness by explicitly modifying native-exotic richness relationships (though see Suding and Gross 2006, Hill and Fischer 2014) and many contingencies need to be addressed in order to provide concrete recommendations on how managers can increase native relative to exotic richness. For example, virtually nothing is known about how seeding density and richness influence native-exotic relationship, or how strongly these effects depend on the identity of species that are sown. A better understanding is also needed of how the effect of seed additions and fire on native-exotic richness relationships varies across the environmental gradients thought to structure these relationships, such as environmental variation in resources, disturbance, and landscape characteristics influencing immigration rates (Tilman 1997, Stohlgren et al. 1999).

Previous studies exploring how management modifies existing native-exotic richness relationships have generally been conducted in sites containing intact native vegetation, and at small spatial scales (< 500 hectares) and across narrow environmental gradients that limit the ability to make general predictions (Suding and Gross 2006, Hill and Fischer 2014). In contrast, we examined native-exotic species richness relationships across 29 sites restored with native prairie seed from bare soil in former agricultural land, within landscapes supporting few native prairie species. These sites were therefore intrinsically seed-limited at the time of restoration and open to colonization by both native and exotic species from seed banks and the surrounding landscape, in addition to the native species included in seed mixes. Importantly, the richness and seeding rate of seed mixes explains the composition and richness of sown species (a subset of native species) across these sites (Grman et al. 2013, 2015). Therefore variation in seed mixes among these sites is likely to impact native-exotic richness relationships, especially if the richness of native and exotic colonizers tends to be correlated in the absence of seed addition

(Meiners et al. 2002). We also examined these relationships at a regional spatial extent (130,000 hectares), similar to many observational studies of natural habitats, but greater than other restoration studies (~50-500 hectares; Foster et al 2002, Suding and Gross 2006, Hill and Fischer 2014). Examining native-exotic richness relationships across a large spatial extent allowed us to more accurately assess the utility of this framework for guiding restoration by spanning more natural variation in edaphic and landscape factors. First, we asked whether native and exotic species richness were correlated across this landscape. Then, we tested whether management, including prescribed fire and seed mix design (richness, density, composition), environmental factors (soil characteristics, landscape context, productivity, light availability, restoration size and age), or interactions among these factors shifted this relationship to favor native species.

Methods

Study system

Our study occurred across 29 grassland restorations in southwestern Michigan (Grman et al. 2014). Between 2003 and 2008, former agricultural land was treated with herbicide and sown with seed of native tallgrass prairie species. Tallgrass prairies are commonly restored using these methods in the Midwestern USA, and are generally managed with periodic prescribed fires to limit growth of woody species, reduce cover and diversity of invasive exotic species, and increase cover and diversity of native prairie species (Packard and Mutel 1997). Sites ranged in size from 0.22 to 39.0 ha (median = 8 ha).

Plant community sampling and species origin

We sampled plant community composition in July-September 2011. At the center of each site in 2011, we established a 45-meter transect and visually estimated the percent cover of all vascular plant species in each of 10 equally spaced 1-m^2 plots. See Grman et al. (2014) for detailed sampling methods.

We calculated native and exotic species richness for each site as the cumulative richness per transect. To do this, we classified each species as *native* if it was present in Michigan prior to European settlement, and otherwise as *exotic*. Four sown species are considered exotic in Michigan, but are native in adjacent states and are members of the target community, so were classified as native here (see Table S3.1). Most species in our dataset classified as exotic in Michigan are also considered exotic throughout North America (Table S3.1), and reclassifying based on continental origin gave equivalent results.

Management and environmental factors

We collected data on management and environmental factors that are likely to influence native-exotic relationships (see Table 3.1 for a summary of these factors and predictions). Management manipulated immigration rates of native species through seed additions, and natural disturbance regimes through prescribed fire. We examined environmental factors related to the immigration rates of native and exotic species, as well as the availability and heterogeneity of resources. Additionally, species declines are common early on in establishing prairie restorations, and either native or exotic species may be lost more rapidly (Sluis et al. 2002, Carter and Blair 2012, Grman et al. 2013). We used restoration age to model potential changes in richness over time.

Table 3.1. Summary of variables used in models to predict native richness relative to exotic richness. Predicted effects, and mechanisms contributing to predicted effects (see Results: *Management and environmental factors* in text for references).

Measured variable	Mean (range)	Description	Mechanism	Prediction
Management				
Seed mix richness	35 (8 - 71)	Number of native species dispersing via seed sowing	Increases native richness, over native species that naturally colonize	positive
Seeding rate (g/m^2)	1.0 (0.68-1.30)	Density of native species dispersing via seed sowing	Increase establishment probability of sown native species	positive
Fire frequency (fires/year)	0.24 (0 - 0.67)	Number of burns per year	Native prairie species are more likely than exotic species to be adapted to fire	positive
Environmental Factors				
Restoration age (years)	5.28 (3-8)	Number of years since sowing	Non-sown species decline over time; exotics may decline because all exotic species are non-sown	positive
Environmental factors related to immigration rates				
Landscape PCA	NA	Principal components axis; higher values indicate greater forest and grassland cover, lower agricultural	Perennial habitats (forest/grassland) occur in disturbed landscapes so they should contribute more exotic than native species	negative
Land-use history	NA	Legacy effects from prior land use (e.g. seedbanks)	Seedbanks from former perennial histories (oldfields, hay fields, pastures) should contribute more exotic than native species	negative
Edge:area ratio (meters/hectares)	0.04 (0.01-0.11)	Ratio of site perimeter:site area	Edge effects increase immigration rates of exotic species	negative
Environmental factors related to resource availability				
Soils PCA	NA	Principal components axis; higher values indicate lower water holding capacity, higher phosphorus and sand	Exotic species more successful in resource-rich sites	positive
Mean biomass (g/m^2)	541 (229 - 872)	Productivity	Exotic species more successful in resource-rich sites	negative
Total % vegetative cover	99 (69 - 116)	Percent cover of all dead and standing biomass	Exotic species more successful in resource-rich sites	negative
Environmental factors related to resource heterogeneity				
CV of water holding capacity	0.10 (0.02 - 0.25)	Heterogeneity of soil moisture retention (along 45 m transect)	Exotic species more successful in high-resource patches in heterogenous sites	negative
CV of biomass	0.28 (0.13 - 0.60)	Heterogenity of site productivity (along 45 m transect)	Exotic species more successful in high-resource patches in heterogenous sites	negative

Management - seed addition and prescribed fire: Native species richness should increase in restorations, relative to exotic species, with the richness and seeding rate of prairie species in seed mixes, and may depend on which species are sown. We collected data on seed mix composition from the seed mix provider (Native Connections, Three Rivers, MI). Sites were sown with between 8 and 71 native prairie species, the majority of which are unlikely to disperse into sites due to regional rarity, and at densities of 0.68-1.30 g seeds/m^2. See Grman et al. (2014) for additional info on composition and seeding rates. Fire is a key natural disturbance in tallgrass prairie, providing pulses of resources such as soil nutrients and light availability, which alter the availability of microsites for colonization (Briggs and Knapp 1995). We consulted landowners for prescribed fire records. To model the effects of prescribed fire, we calculated fire frequency as the number of fires divided by restoration age.

Environmental factors related to immigration rates: Both surrounding landscape composition and land-use history can affect immigration rates of non-sown native and exotic species (Hobbs and Huenneke 1992, Meiners et al. 2004), and therefore may alter the ratio of native to exotic species richness (Lonsdale 1999, Simberloff 2009). To assess how different landscapes influenced immigration rates, we identified the area of forest, grassland, wetland, row crops, and developed land within 500 meters of the center of each site in ArcGIS (Grman et al. 2013). We simplified data on landscape composition through principal components analysis (PCA). On the first axis (landPC1), which explained 59% of the variation in landscape composition, higher values represented greater forest and grassland cover, and lower cover of agricultural uses. We predicted that because restorations occur in disturbed post-agricultural landscapes, the species pool in these landscapes would be dominated by exotic species (Parker et al. 2010, Jauni and

Hyvönen 2012). As a result, landscapes with greater cover of established habitats (forest and grassland) would support larger exotic populations and greater propagule pressure, and restorations in these landscapes would therefore have proportionally higher exotic (and lower native species) richness. Propagules of non-sown species also originate in the seed- or budbank of restoration sites, which may vary depending on land-use history. We consulted landowners to determine the immediate pre-restoration land use of each site, which we classified as row-crops (generally tillage agriculture, some no-till) or perennial grassland (hay, pasture, and old fields). Similarly to our landscape prediction, we predicted that sites restored from perennial grasslands (hay, pasture, old fields) would have a lower proportion of native species richness. Finally, we also calculated the perimeter:area ratio of each site in ArcGIS. We predicted that edge effects in sites with higher perimeter:area ratios would enhance invasion from surrounding habitats, and lead to a lower proportion of native species richness (With 2002 Conservation Biology, Vila and Ibanez 2011).

Environmental factors related to resource availability: Native and exotic species may respond differently along resource gradients, or to spatial variation in resources (Davies et al. 2005, Carboni et al. 2010, Brummer et al. 2016). Grassland plant communities are most strongly influenced by soil resources, productivity, and light availability (Briggs and Knapp 1995, Borer et al. 2014). Exotic species may be more successful than native species in high resource environments (Seabloom et al. 2015), so we predicted that native species richness would be higher relative to exotic species richness in low resource environments. To assess soil resources, we sampled eight 20 cm × 3 cm^2 soil cores at each plot (10 plots per site). We pooled samples for each plot and measured water-holding capacity in the lab as the proportional difference of saturated to oven-dried weight (after Brudvig and Damschen 2011). We calculated three measures of site-level resource availability – soil resources, productivity, and light availability. To assess site-level resource availability, we pooled samples for each site and analyzed soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, and pH (Brookside Laboratories, New Knoxville, OH, USA). We simplified site-level soils data by conducting a principal components analysis (PCA). On the first axis (soil PC1), which explained 56% of the variation in soils data, higher values indicated sites with sandier soils, low water holding capacity, and higher phosphorus. To assess productivity, we clipped, dried at 155° C, and weighed all above-ground biomass in each 1-m^2 plot. We used mean biomass/m^2 as a measure of site-level productivity. We used the sum of total percent vegetative cover and litter cover, which were assessed visually in each plot and together ranged from 69-116%, as an inverse measure of light availability. Finally, heterogeneous environments have high-resource patches that may favor exotic species (Shea and Chesson 2002). As in low resource environments, we predicted that native species richness would be higher relative to exotic species richness in more homogeneous environments. We used the coefficient of variation in water holding capacity and biomass among plots to model heterogeneity soil resources and productivity, respectively.

Data analysis

To test whether native and exotic species richness were correlated across sites, we calculated Pearson's r. While not central to the goals of this study, null models are commonly applied in similar studies; therefore, we compared observed native-exotic correlations to a null distribution based on random assembly from a species pool with a fixed ratio of native to exotic species (Fridley et al. 2004, Herben et al. 2004), and include these results in the Appendix (Figures S3.5, S3.6).

We examined whether management and environmental factors shifted the native-exotic species richness relationship to favor native species. First, we regressed native richness on exotic richness and calculated least-squared residuals. Then, we conducted model selection with AICc (Burnham and Anderson 2002) on a set of models with these residuals as the response variable, and in which management, environmental factors, and their interactions predicted these residuals (full model set in Table S3.2). This model set contained three types of additive models: 1) models that included at least one management variable as a predictor (Table 3.1; seed mix richness, seeding rate, fire frequency); 2) models that included a single environmental variable (Table 3.1; restoration age, perimeter:area ratio, landscape PCA, land-use history, soils PCA, aboveground biomass, % vegetative cover, CV of water holding capacity, and CV of biomass) as a predictor; and 3) models that included at least one management variable plus at least one environmental variable. We also included two types of interaction models to test whether 1) the effect of management varies across environments (e.g., fire x productivity, 2) or the effect of individual management variables depends on other management variables (e.g., seed mix richness x seeding rate). Predictors in these models were not strongly correlated ($r < 0.55$, mostly < 0.30; Table S3.3), and variance inflation factors were all < 4 .We also included an intercept-only model as a baseline of no effect. We examined the direction and strength of standardized parameter estimates in all models with ‘considerable support’ (dAIC ≤ 4.0), which we refer to as ‘competitive models’ and use for inference, but also report models with ‘considerably less support’ (4.0 < dAIC ≤ 7.0) (Burnham and Anderson 2002) in Table 3.2.

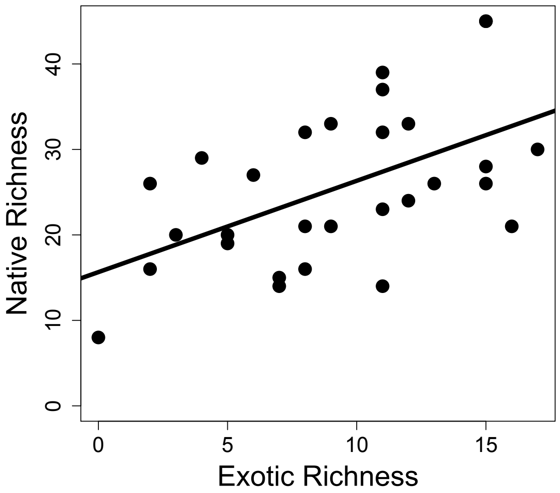
Because we found strong support for a model in which the effect of seed mix richness on native richness depended on seeding rates (see Table 3.2), we conducted an additional model selection analysis to test whether specific aspects of seed mix composition related to native-exotic richness relationships. Specifically, we focused on variation in the abundance of plant functional groups, or species grouped by shared functional traits, because they are known to have different establishment probabilities (Tilman 1997, Symstad 2000). Additionally, managers can adjust the seeding rates and richness of functional groups that are most likely to increase native richness. We sorted seed mix composition into four functional groups: C_3 graminoids (including Cyperaceae and Juncaceae), C_4 graminoids (all Poaceae), nitrogen-fixers (forbs and two sub-shrubs, mostly Fabaceae but including Rhamnaceae; hereafter "legumes"), and non-nitrogen-fixing forbs (hereafter "forbs") (Table S3.4). Two sites lacked detailed seed mix composition data, so we conducted this analysis on a restricted dataset of 27 sites. We constructed a model set, as above, where each model predicted the residuals of regressing native on exotic species richness. First, we built four individual models, testing whether the effect of the species richness of each functional group on these residuals depended on the total seeding rate of species within that same functional group (e.g., richness of forbs x rate of forbs). We also modeled the interaction of total seed mix richness with the seeding rate of each functional group (e.g., total seed mix richness x forb seeding rate), and the total seeding rate with the richness of each functional group (e.g., forb seed mix richness x total seeding rate). Finally, because dominance of C_4 grasses may reduce diversity by limiting the establishment of other sown species (Howe 1994), we also modeled the interaction between C_4 grass seeding rate and the richness of each functional group (Dickson and Busby 2009). Then, we compared this more detailed set of seed mix composition models, as well as the original seed mix model, with AICc, as described above.

Finally, because native richness was lower in older sites (see Table 3.2), we controlled for restoration age in all models. In summary, each seed composition model had four terms: richness of either the total seed mix or a signal functional group in the seed mix, the seeding rate of the total seed mix or a single functional group in the seed mix, the interaction between rate and richness, and restoration age.

Results

Native species richness was positively correlated with exotic species richness across our sites (Pearson's r = 0.54, $p < 0.01$) (Figure 3.1). However, management variables influenced the residuals of the native-exotic regression. Seed mix richness increased native richness most strongly at high seeding rates; at low seeding rates, seed mix richness had no effect on native richness (Model 1 in Table 3.2, seed mix richness x seeding rate, $p < 0.01$; Figure 3.2). While

Figure 3.1. Native and exotic species richness was positively correlated across 29 prairie restorations. Pearson's r = 0.54, p <0.01.

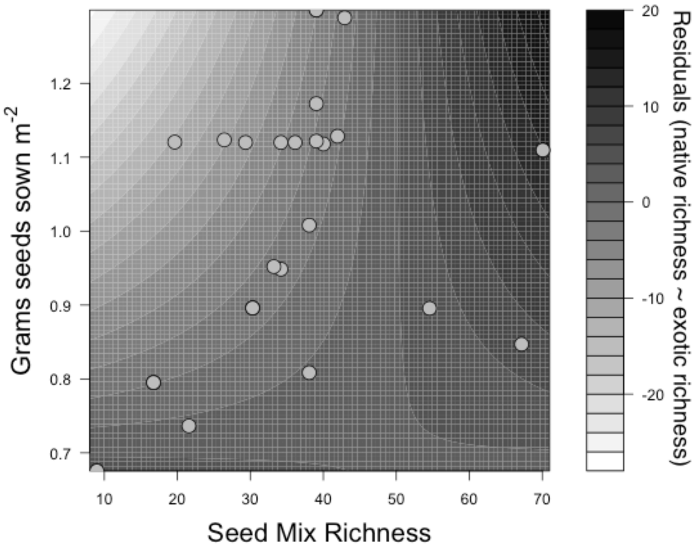


native richness was strongly influenced by seed mixes, we found that more frequent fire increased native species richness only weakly (Table S3.2, all models including a term for fire, ΔAICc ≥ 8.5; Figure 3.3). In addition, older restorations had proportionally lower native richness than younger restorations in a competitive model (ΔAICc < 4.0), which included the main effects of seed mix richness and seeding rates (Model 2 in Table 3.2, ΔAICc = 2.6, adj-R^2 = 0.43; Figure 3.4). This pattern was apparently driven by loss of native, and not exotic species over time (Figure S3.1a). There was little evidence that abiotic environmental conditions modified the native-exotic relationship (Tables 3.2, S3.1), suggesting that modifying native-exotic richness relationships are largely under the control of managers.

Table 3.2. Top management and environmental models predicting native species richness after controlling for association with exotic species richness (residuals of linear regression model: native species richness ~ exotic species richness) selected by AICc. Only models with dAICc < 7.0 are shown. Standardized estimates are shown (***p<0.001, **p<0.01, *p<0.05). Terms not in model indicated with a dash (-). *Mix SR* = seed mix richness; *Mix Rate* = seeding rate (g/m^2); see Table 2.1 for Covariate definitions.

Model	Covariate	Mix SR	Mix Rate	Mix SR x Rate	Covariate	logLik	dAICc	df	weight	R^2
1	-	5.91***	-3.36*	3.65**	-	-88.7	0	5	0.59	0.48
2	Age	4.14**	-3.80**	-	-2.72*	-90	2.6	5	0.16	0.43
3	CV Biomass	4.30**	-5.17**	-	-2.38	-91.5	5.6	5	0.04	0.37
4	Biomass	4.60**	-4.57**	-	1.99	-91.5	5.7	5	0.03	0.37
5	-	4.83**	-4.13**	-	-	-93	5.8	4	0.03	0.33
6	Land PCA	5.25***	-3.99**	-	-1.85	-91.7	6.1	5	0.03	0.36
7	Edge:Area	5.05***	-4.27**	-	1.78	-91.8	6.1	5	0.03	0.36

Figure 3.2. Native species richness was higher than predicted from the native-exotic richness relationship, in sites sown with many species at high rates. Heat map showing response of residuals from native SR~exotic SR regression to interactive effect: seed mix richness x seeding rate, $p < 0.01$ (see Model 1 in Table 2). Darker shading = higher proportional native richness (i.e., positive residuals); lighter shading = lower proportional native richness (i.e., negative residuals). Points in gray show coverage of data over predicted relationship.



The effects of seed mix richness and seeding rates on the relative number of native species compared to exotics were driven primarily by forb species (Table 3.3, Figures 3.5a-c). Among seed mix composition models, modeling the interaction between forb richness and total seeding rate predicted native species richness as well modeling the interaction between total richness and total seeding rate (Table 3.3; *Forb SR-Mix Rate*: ΔAICc = 0.4, adj-$R^2 = 0.52$; *Mix SR-Mix Rate*: ΔAICc = 0.0, adj-$R^2 = 0.53$). As with total seeding richness and rate (Figure 3.2), forb seeding richness also increased native richness only at high total seeding rates (Figure 3.5c), although interactions between richness and rates in this restricted dataset were only marginally significant (Table 3.3; total seed mix richness x total seeding rate, p = 0.052; forb seed mix richness x total seeding rate, p = 0.054). Forb seeding rates did not predict native richness as well as forb richness, based on AICc. The next two highest-ranked models included interactions of forb seeding rates with total seed mix richness (Figure 3.5b, Table 3.3; *Mix SR-Forb Rate:* ΔAICc = 3.6, adj-R^2 = 0.46) and forb richness (Figure 3.5a, Table 3.3; *Forb SR-Forb Rate:* ΔAICc = 4.6, adj-R^2 = 0.44). Among other functional groups, only C_3 grass models predicted native richness moderately well (Table 3.3; *C_3 SR-Mix Rate:* ΔAICc = 6.0, adj-R^2 = 0.41, *Mix SR-C_3 Rate:* ΔAICc = 7.2, adj-R^2 = 0.38; Figures 3.5e,f). Contrary to expectations, the effect of functional group richness did not depend on C_4 grass seeding rate (Table 3.3; all models including a term for C_4 grass seeding rate, ΔAICc >10).

Figure 3.3. Native-exotic richness relationship is not modified by fire frequency. Native richness increases with fire frequency, but effect is only marginally significant (a); fire frequency, p = 0.09. The effect of fire frequency is not significant when controlling for seed mix richness and seeding rates (b); fire frequency, p = 0.70.

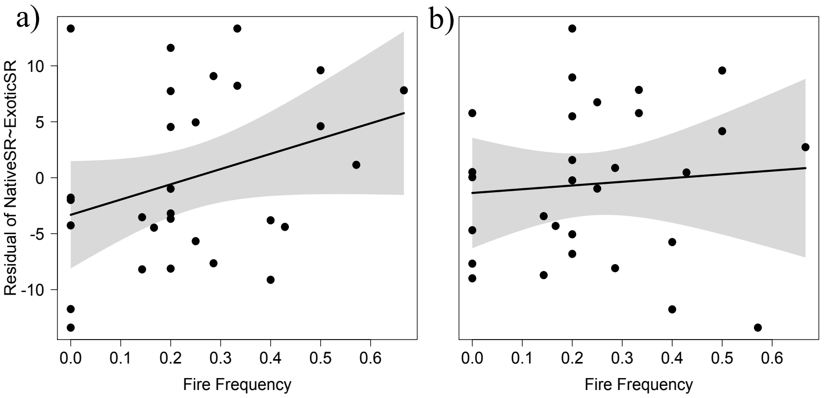
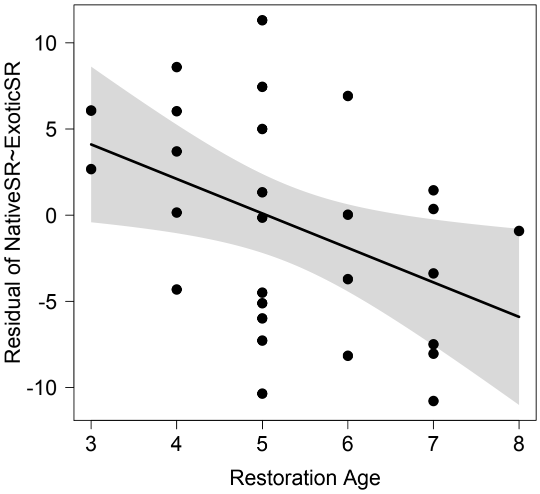


Figure 3.4. In older sites, native species richness is lower than predicted from native-exotic richness relationship. Partial residual plot; restoration age, p = 0.02; Model 2 in Table 3.2.



Discussion

One of the greatest restoration challenges is designing strategies to increase native species diversity while also discouraging exotic species (Matthews and Spyreas 2010, Brudvig 2011, Suding 2011). It is a challenge in part because native and exotic species may respond to the same environmental drivers in both established (Stohlgren et al. 1999) and successional (Meiners et al. 2004) natural habitats, and may respond similarly during restoration (Suding and Gross 2006). We found that, while native and exotic species richness was positively correlated across 29 prairie restorations, sites sown with more species at higher rates had higher native species richness than predicted from this underlying correlation. In contrast, sites sown with high densities of few species had lower proportions of native species than predicted by native-exotic correlations. This pattern was primarily driven by the forb component of seed mixes, and to a lesser extent by the C_3 graminoid component.

Figure 3.5. Interaction between seed mix richness and seeding rate is driven largely by forbs in seed mix, and to a lesser extent by C_3 grasses. Heat map showing response of residuals from native SR~exotic SR regression to interactive effect of of the seed mix richness and seeding rate of important functional groups, and between these functional groups and the total richness and rate of seed mixes (see models in Table 3.3). Darker shading = higher proportional native richness (i.e., positive residuals from native SR ~ exotic SR regression); lighter shading = lower proportional native richness (i.e., negative residuals). Interactions between richness and seeding rate of forbs (a), and C_3 grasses (d); interactions between *total seed mix richness* and seeding rate of forbs (b) and C_3 grasses (e); interactions between *total seeding rate* and seed mix richness of forbs (c), C_3 grasses (f). See Figure S2 for interactions with legumes and C_4 grasses.

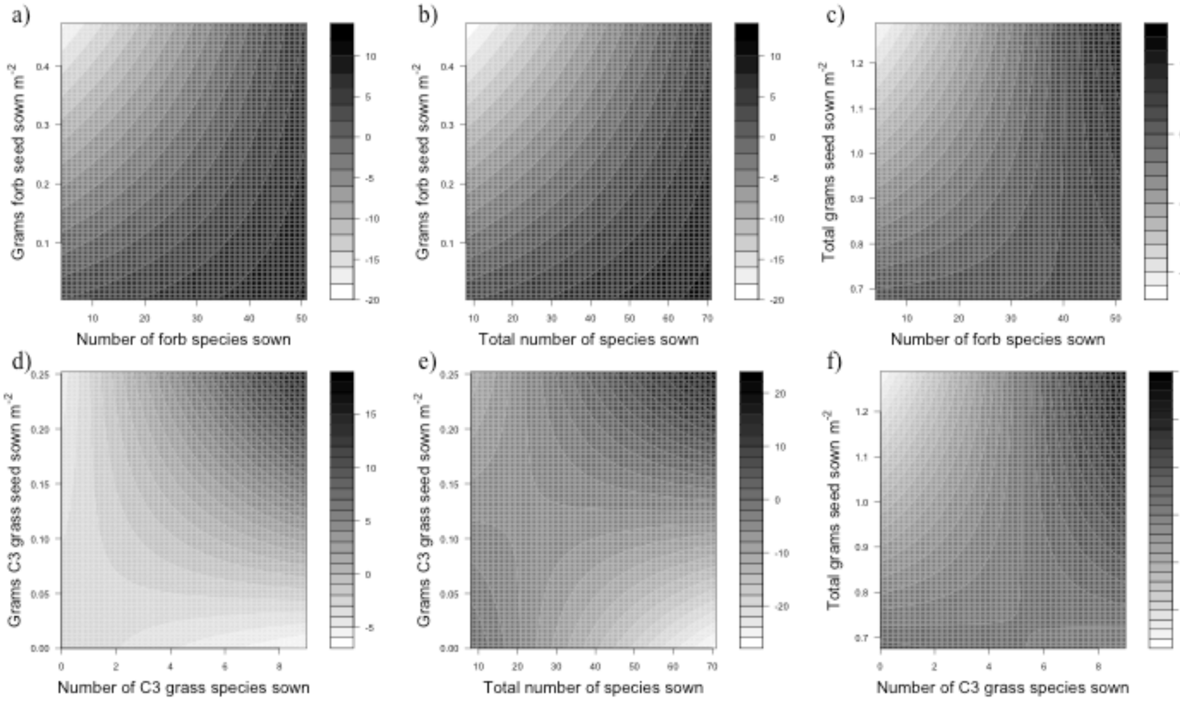


Table 3.3. Seed composition models predicting native species richness after controlling for association with exotic species richness (residuals of linear regression model: native speices richness ~ exotic species richness) selected by AICc. All models shown, but models with dAIC>10.0 have little or no support, while those <4.0 all have reasonable support. Standardized estimates are shown (***p<0.001, **p<0.01, *p<0.05, +p<0.10). Terms not in model indicated with a dash (-). *Mix SR* = seed mix richness; *Mix Rate* = seeding rate (g/m^2); *Func=functional group.* See *Figures 3.5* and *S3.2* for form of interactions.

Model	Mix SR	Mix Rate	Func SR	Func Rate	Func SR x Func Rate	Mix SR x Func Rate	Func SR x Mix Rate	Mix SR x Mix Rate	Age	delta AICc	df	weight	R^2
Mix SR x Mix Rate	5.00***	-3.77**	-	-	-	-	-	2.53+	-2.48*	0.0	6	0.45	0.53
Forb SR x Mix Rate	-	-3.84**	5.12***	-	-	-	2.68+	-	-2.64*	0.4	6	0.36	0.52
Mix SR x **Forb** Rate	4.83**	-	-	-4.84**		1.53	-	-	-4.17*	3.6	6	0.07	0.46
Forb SR x Rate	-	-	4.74**	-4.72**	1.61	-	-	-	-4.24*	4.6	6	0.05	0.44
C3 SR x Mix Rate	-	-2.37+	3.30*	-	-	-	2.27	-	-1.67	6.0	6	0.02	0.41
Mix SR x **C3** Rate	-0.48	-	-	3.29	-	4.27*	-	-	-3.42**	7.2	6	0.01	0.38
Legume SR x Mix Rate	-	-4.05*	3.82*	-	-	-	1.48	-	-3.58*	7.5	6	0.01	0.37
Mix SR x **Legume** Rate	4.58*	-	-	-2.70+	-	2.88	-	-	-1.52	9.1	6	0.005	0.33
C4 SR x Mix Rate	-	-3.25*	3.24*	-	-	-	1.36	-	-4.67**	9.2	6	0.005	0.33
Legume SR x Rate	-	-	5.00*	-5.01**	2.23	-	-	-	-3.26*	9.7	6	0.004	0.32
Forb SR x **C4** Rate	-	-	1.72	-3.29*	-2.67	-	-	-	0.01	10.4	6	0.003	0.30
Mix SR x **C4** Rate	1.65	-	-	-3.28+	-	-2.41	-	-	-0.08	11.1	6	0.002	0.28
INTER-CEPT	-	-	-	-	-	-	-	-		12.9	2	<0.001	0
C3 SR x **C4** Rate	-	-	1.19	-2.89	-1.56	-	-	-	-0.20	13.0	6	<0.001	0.23
C3 SR x Rate	-	-	2.20	1.32	1.79	-	-	-	-1.48	13.6	6	<0.001	0.21
Legume SR x **C4** Rate	-	-	0.59	-3.65+	-1.52	-	-	-	-1.27	14.4	6	<0.001	0.19
C4 SR x Rate	-	-	1.39	-2.50	-0.57	-	-	-	-2.17	14.9	6	<0.001	0.18

Management favors native richness

Consistent with large-scale observational studies in natural habitats, native and exotic species richness were positively correlated across our sites. Yet, our results suggest that managers can modify the native-exotic richness relationship to favor native species by using seed mixes that increase the immigration rates of native species. Proportional increases in native species required not only the immigration of many native species (e.g, > 50 species sown), but also sowing at high densities (e.g, > 1 g seed/m^2). These high seeding rates in species-rich mixes may be necessary to overcome demographic barriers to population establishment, especially for forbs. While the overall seeding rate of forbs increased with forb richness (Table S3.5), the seeding rates of individual species are often low due to the high cost of many forb species. At low overall seeding rates, the number of colonizing individuals of many forb species is probably too low to establish viable populations, especially if further limited by abiotic conditions (Grman et al. 2015). The importance of forb species for driving native richness may also be in part because forbs account for the majority of the variation in seed mix richness and seeding rates (Grman et al. 2015; Table S3.4). The influence of C_3 graminoids and legumes on native richness was similar to the influence of forbs, but variation (or maximum amounts) in the richness and seeding rate of C_3 graminoids and legumes may not be great enough to allow for detectable effects on overall native richness (*forbs*: 4-51 species, 0.003-0.473 g/m^2; *C_3 graminoids*: 0-9 species, 0-0.252 g/m^2; *legumes*: 1-8 species, 0.001-0.126 g/m^2; Table S3.4).

In contrast to sowing greater densities of many species, sowing greater densities of fewer species was associated with proportionally lower native richness. Highly competitive C_4 grasses dominate low-richness seed mixes (Table S3.4). C_4 grasses can reduce the richness of other native and exotic species when sown at high rates (Dickson and Busby 2009). We tested for overall effects of C_4 grass richness and rate in seed mixes, and whether the effect of functional group richness depended on C_4 grass seeding rate. Because C_4 grass richness is consistently low (3-6 species) and seeding rates consistently high (0.392-0.785 g/m^2), there was likely insufficient variation at biologically meaningful ranges (e.g., no low C_4 seeding rates or high C_4 richness) to explain differences in native richness. From a management perspective, this suggests that investing in high seeding rates of many forb species benefits native diversity. When the level of investment required for both higher seeding rates and more species is not feasible, however, appreciable increases in native richness may be limited. In fact, when sowing mixes with low to intermediate richness (< ~ 40 species), our results suggest that sowing at low rates (< ~ 0.8 grams seed/m^2) may lead at most to modest proportional increases in native richness, but increasing seeding rates beyond 1.0 grams seed/m^2 is likely to lead to decreased native richness.

Surprisingly, we detected little evidence that fire, one of the most common management tools, influences the relative proportion of natives. This result contrasts with similar studies, where both seed additions and fire have increased native, relative to exotic richness (Suding and Gross 2006, Hill and Fischer 2014). These studies, however, occurred in later successional grasslands. For example, Suding and Gross (2006) imposed burning and seed addition treatments across a degraded prairie landscape in southwestern Michigan in which native and exotic richness was positively correlated. Burning alone broke the correlation, seed addition alone increased native richness only at intermediate exotic richness, while the combination of seed addition and burning increased native richness but maintained the positive correlation (Suding and Gross 2006). Colonization rates of exotic species may be higher in earlier-successional systems such as ours, overwhelming any negative impact of fire on exotic species.

The impact of seed sowing may fade over time

While our results showed how seed sowing can modify the native-exotic richness relationship to favor native species, we also found that native-exotic richness relationships shifted to favor exotic species over time. This shift was due to *declining* native richness, not *increasing* exotic richness, with restoration age. Species richness often declines over time during prairie restoration (Sluis 2002, Middleton et al. 2010, Grman et al. 2013), although other studies have pointed to reductions in exotic and not native richness as the cause of this pattern (Heslinga and Grese 2010, Carter and Blair 2012). In our system, greater loss of native species may be due to variation in the rates, richness, and composition of seed mixes with restoration age, or because successional processes influenced native vs. exotic species differently. We find some support for this first idea, as seed mixes in older restorations contain fewer forbs and C_3 grasses, and more C_4 grasses (Table S3.5) and these differences may influence the development and maintenance of native richness over time. However, independent of these differences, restoration age predicted lower native richness in models (Table 3.3). This suggests that restoration age and seed mix properties have independent effects on native richness.

As further evidence that loss of native richness is not simply a function of seed mix properties, the richness of non-sown native species appears to be more strongly correlated with restoration age than the richness of sown native species (Grman et al. 2013, Figure S3.1b). In the landscapes where these restorations occur, native species may colonize at low rates because propagule sources are rare. As a result, non-sown native species may be prone to localized extinctions over time. In contrast, exotic species occur at higher densities in the landscape and local populations may be augmented or periodically rescued through repeat dispersal events (Gotelli 1991). Alternately, dominant community members, such as the C_4 prairie grass

Andropogon gerardii, may exclude native species more strongly than exotics (Howe 1994, Heslinga and Grese 2010, Carter and Blair 2012), but we found no evidence for this effect (Figure S3.3). We therefore suggest that native species declines are a function of low recurring propagule inputs.

Conclusions and management implications

Additional work in our system has compared a wide range of management and environmental factors to explain variation in both sown native (Grman et al. 2013, 2014, 2015) and invasive exotic species (see Chapter 4). The restoration of diverse sown (native) communities is limited somewhat by soil moisture (Grman et al. 2014), but largely influenced by sowing more species, and greater densities of forbs (Grman et al. 2013, 2015). In turn, exotic invasive species are limited by diversity and dominance of sown species, but also strongly influenced by land-use history legacies (see Chapter 4). Together, this suggests that managers can influence the dynamics between native and exotic species through seed sowing, but also that the effectiveness of the sown community for resisting invasion may be limited under certain conditions (e.g., sites with low soil moisture, or certain land-use histories). Here we contribute to our understanding of how restored grassland communities assemble by explicitly considering the relationship between native and exotic species richness. Across a wide range of hypothesized drivers, including many that are difficult for managers to manipulate (e.g., soil properties), our results suggest that modifying native-exotic richness relationships to favor native species is largely determined by seed mix design, which managers control. However, practical constraints (i.e., financial costs) may limit this control. Obtaining a large amount of seed of many forb species, which our results suggest is necessary to increase native richness, generally requires a significant investment of time or money. This investment is clearly warranted when increasing native richness is the goal. When managers lack financial or labor resources to sufficiently invest in the forb component of seed mixes, however, it may be difficult to increase native richness, relative to exotic richness, and restoration goals may need to be adjusted to simply aim for native dominance, instead of a diverse native community. Restorations with low to intermediate native plant diversity still provide many important ecosystem services and may provide habitat for important wildlife species (e.g., grassland birds) (Werling et al. 2014).

Positive native-exotic richness relationships are nearly ubiquitous in both managed and unmanaged plant communities, but this does not necessarily represent a limitation for restoration. First, native species richness was generally high at our sites, between 1.2 and 12.9 times higher than exotic species richness (median = 2.8 times higher), and the relative abundance of native species was also high (median = 84%). Therefore, managers generally restored communities largely composed of native species. Second, the correlation between native and exotic richness does not necessarily predict negative impacts of exotic species on community and ecosystem processes (Seabloom et al. 2013). The ability for managers to increase native relative to exotic richness is especially impactful if those increases translate into reductions in the dominance of exotic species. In these 29 sites, exotic dominance was lowest in sites where native richness was higher than predicted by the native-exotic richness relationship (Figure S3.4). Therefore, while some exotic species will inevitably be a component of both managed and unmanaged plant communities, the presence of exotic species, by itself, need not be a major concern for managers (D’Antonio and Myerson 2002, Hobbs et al. 2009). In fact, our results here and elsewhere (Grman et al. 2013) suggest that managers have a great deal of influence in restoring plant communities with largely desirable qualities (e.g., are dominated by a diversity of native species).

Acknowledgements

Insights from Jeff Conner improved the interpretation of results. Thank you to Beth Miller for help coding the null model distribution. Portions of this work was funded by USDA-NIFA grant 2013-67011-21281.

APPENDIX

Table S3.1. Origin and abundance of species in dataset. *In seed mix but not native to Michigan. Y*, in seed mix but frequently naturally colonizes sites.

Species	**Origin**	**Mean Cover**	**In seed mix?**
Abutilon theophrasti	exotic	0.02%	N
Agrostis gigantea	exotic	0.08%	N
Alliaria petiolata	exotic	0.05%	N
Arctium minus	exotic	0.03%	N
Barbarea vulgaris	exotic	0.09%	N
Bromus inermis	exotic	2.38%	N
Centaurea stoebe	exotic	0.58%	N
Cerastium fontanum	exotic	0.04%	N
Chenopodium album	exotic	0.00%	N
Chenopodium sp.	exotic	0.00%	N
Cirsium arvense	exotic	1.00%	N
Crepis capillaris	exotic	0.01%	N
Crepis sp.	exotic	0.00%	N
Dactylis glomerata	exotic	0.77%	N
Daucus carota	exotic	1.44%	N
Dianthus armeria	exotic	0.02%	N
Digitaria sp.	exotic	0.26%	N
Elymus repens	exotic	3.31%	N
Frangula alnus	exotic	0.01%	N
Hieracium sp.	exotic	2.98%	N
Hypericum perforatum	exotic	0.22%	N
Hypochaeris radicata	exotic	1.42%	N
Leucanthemum vulgare	exotic	0.01%	N
Lonicera sp.	exotic	0.00%	N
Medicago lupulina	exotic	0.01%	N
Medicago sativa	exotic	0.01%	N
Melilotus sp.	exotic	0.03%	N
Mollugo verticillata	exotic	0.03%	N
Morus alba	exotic	0.14%	N
Phleum pratense	exotic	0.02%	N
Plantago lanceolata	exotic	0.97%	N
Plantago major	exotic	0.01%	N
Plantago sp.	exotic	0.02%	N
Poa pratensis	exotic	24.10%	N
Polygonum aviculare	exotic	0.00%	N
Polygonum persicaria	exotic	0.01%	N
Potentilla argentea	exotic	0.01%	N
Potentilla recta	exotic	0.20%	N

Table S3.1 (cont'd)

Species	**Origin**	**Mean Cover**	**In seed mix?**
Potentilla sp.	exotic	0.03%	N
Rosa multiflora	exotic	0.00%	N
Rumex acetosella	exotic	1.20%	N
Rumex crispus	exotic	0.31%	N
Saponaria officinalis	exotic	0.02%	N
Setaria sp.	exotic	0.05%	N
Silene latifolia	exotic	0.28%	N
Solanum carolinense	exotic	0.95%	N
Stellaria media	exotic	0.05%	N
Taraxacum officinale	exotic	0.34%	N
Trifolium arvense	exotic	0.09%	N
Trifolium pratense	exotic	3.89%	N
Trifolium repens	exotic	0.05%	N
Trifolium sp.	exotic	0.64%	N
Verbascum thapsus	exotic	0.08%	N
Veronica arvensis	exotic	0.00%	N
Veronica serpyllifolia	exotic	0.03%	N
Veronica sp.	exotic	0.00%	N
Vicia villosa	exotic	0.01%	N
Acalypha rhomboidea	native	0.00%	N
Acer sp.	native	0.01%	N
Achillea millefolium	native	1.36%	Y*
*Agastache foeniculum**	native	0.01%	Y
Agastache nepetoides	native	0.03%	Y
Ambrosia artemisiifolia	native	0.24%	N
Andropogon gerardii	native	45.31%	Y
Anemone cylindrica	native	0.02%	Y
Anenome sp.	native	0.13%	N
Antennaria parlinii	native	0.00%	N
Apocynum cannabinum	native	0.05%	N
Aquilegia canadensis	native	0.01%	Y
Arnoglossum atriplicifolium	native	0.66%	Y
*Artemesia ludoviciana**	native	0.06%	N
Asclepias syriaca	native	0.37%	Y*
Asclepias tuberosa	native	0.14%	Y
Asplenium platyneuron	native	0.00%	N
Botrychium dissectum	native	0.00%	N
Bouteloua curtipendula	native	1.73%	Y
Brickellia eupatorioides	native	0.07%	Y
Carex bicknellii	native	1.08%	Y

Table S3.1 (cont'd)

Species	Origin	Mean Cover	In seed mix?
Carex brevior	native	0.27%	Y
Carex sparganioides	native	0.02%	Y
Carex swanii	native	0.11%	N
Celtis occidentalis	native	0.01%	N
Chamaecrista fasciculata	native	0.01%	Y
Conyza canadensis	native	0.03%	N
Coreopsis lanceolata	native	0.14%	Y
Coreopsis palmata	native	0.10%	Y
Coreopsis tripteris	native	0.88%	Y
Crataegus sp.	native	0.01%	N
Cyperus erythrorhizos	native	0.00%	N
Cyperus lupulinus	native	0.01%	N
Dalea purpurea	native	0.03%	Y
Desmodium canadense	native	1.00%	Y
Desmodium ciliare	native	0.10%	N
Desmodium obtusum	native	0.02%	N
Desmodium paniculatum	native	0.03%	N
Desmoidum hybrid2	native	0.08%	N
Dichanthelium clandestinum	native	0.82%	N
Dichanthelium lindheimeri	native	0.00%	N
Dichanthelium meridionale	native	0.01%	N
Dichanthelium oligosanthes	native	0.01%	N
Digitaria cognatum	native	0.10%	N
Echinacea pallida	native	0.06%	Y
Echinacea purpurea	native	3.30%	Y
Elymus canadensis	native	2.39%	Y
Elymus virginicus	native	0.07%	Y
Epilobium ciliatum	native	0.01%	N
Equisetum sp.	native	0.02%	N
Erigeron sp.	native	0.46%	N
Euphorbia corollata	native	0.02%	N
Euthamia graminifolia	native	1.61%	Y*
Fragaria virginiana	native	0.00%	N
Fraxinus sp.	native	0.00%	N
Galium aparine	native	0.00%	N
Galium pilosum	native	0.01%	N
Geum canadense	native	0.05%	N
Geum sp.	native	0.05%	N
Gnaphalium obtusifolium	native	0.10%	N
Habenaria lacera	native	0.00%	N

Table S3.1 (cont'd)

Species	**Origin**	**Mean Cover**	**In seed mix?**
Helenium autumnale	native	0.00%	Y
Helianthus grosseserratus	native	0.02%	Y
Helianthus maximilianii	native	0.01%	Y
Helianthus mollis	native	0.15%	Y
Helianthus occidentalis	native	0.06%	Y
Helianthus strumosus	native	0.08%	Y
Heliopsis helianthoides	native	1.65%	Y
Heuchera sp.	native	0.01%	Y
Hypericum ascyron	native	0.00%	Y
Hypericum punctatum	native	0.00%	N
Hypericum sp.	native	0.02%	N
Juglans sp.	native	0.02%	N
Juncus tenuis	native	2.90%	N
Koeleria macrantha	native	0.01%	Y
Lactuca canadensis	native	0.25%	N
Lactuca sp.	native	0.00%	N
Lespedeza capitata	native	0.06%	Y*
Lespedeza hirta	native	0.03%	N
Liriodendron tulipifera	native	0.03%	N
Lobelia inflata	native	0.02%	N
Lupinus perennis	native	0.26%	Y
Lycopus sp.	native	0.07%	Y
Monarda fistulosa	native	6.25%	Y*
Monarda punctata	native	0.02%	Y
Muhlenbergia frondosa	native	0.06%	N
Muhlenbergia schreberi	native	0.00%	N
Oenothera biennis	native	0.19%	Y*
Oenothera sp.	native	0.01%	N
Onoclea sensibilis	native	0.12%	N
Oxalis sp.	native	0.13%	N
Panicum dichotomiflorum	native	0.00%	N
Panicum virgatum	native	3.56%	Y
*Parthenium integrifolium**	native	0.18%	Y
Parthenocissus quinquefolia	native	0.08%	N
Penstemon digitalis	native	0.56%	Y
Phalaris arundinacea	native	0.01%	N
Phytolacca americana	native	0.02%	N
Plantago rugelii	native	0.01%	N
Polygala polygama	native	0.00%	N
Polygonum pensylvanicum	native	0.00%	N

Table S3.1 (cont'd)

Species	**Origin**	**Mean Cover**	**In seed mix?**
Populus deltoides	native	0.08%	N
Populus grandidentata	native	0.02%	N
Populus tremuloides	native	0.01%	N
Potentilla simplex	native	0.11%	N
Prunus serotina	native	0.00%	N
Pycnanthemum virginianum	native	0.06%	Y
Ranunculus abortivus	native	0.00%	N
Ratibida pinnata	native	4.12%	Y
Rhynchospora capitellata	native	0.00%	N
Ribes sp.	native	0.00%	N
Rubus allegheniensis	native	0.48%	N
Rubus flagellaris	native	2.04%	N
Rubus occidentalis	native	1.46%	N
Rudbeckia hirta	native	4.05%	Y
Rudbeckia subtomentosa	native	0.06%	Y
Rudbeckia triloba	native	0.74%	Y
Salix sp.	native	0.00%	N
Sassafras albidum	native	0.05%	N
Schizachyrium scoparium	native	25.63%	Y
Senna hebecarpa	native	0.09%	Y
Silphium integrifolium	native	0.12%	Y
Silphium perfoliatum	native	0.01%	Y
Solanum ptychanthum	native	0.01%	N
Solidago canadensis	native	16.83%	N
Solidago rigida	native	0.99%	Y
Solidago rugosa	native	0.10%	N
Solidago speciosa	native	1.86%	Y
Sorghastrum nutans	native	31.82%	N
Symphyotrichum lateriflorum	native	0.18%	N
Symphyotrichum novaeangliae	native	0.45%	Y
Symphyotrichum oolentangiense	native	0.08%	Y
Symphyotrichum pilosum	native	0.69%	Y*
Symphyotrichum puniceum	native	0.01%	N
Symphyotrichum urophyllum	native	0.07%	Y
Toxicodendron radicans	native	0.22%	N
Tradescantia ohiensis	native	0.11%	Y
Tridens flavus	native	0.36%	N
Triodanis perfoliata	native	0.00%	N
Ulmus sp.	native	0.05%	N
Verbena hastata	native	0.00%	Y

Table S3.1 (cont'd)

Species	**Origin**	**Mean Cover**	**In seed mix?**
*Verbena stricta**	native	0.03%	N
Veronicastrum virginicum	native	0.02%	Y
Viola striata	native	0.01%	N
Vitis aestivalis	native	0.01%	N
Vitis riparia	native	0.14%	N
Zizia aurea	native	0.16%	Y

Table S3.2. Full model set predicting residuals of native richness~exotic richness regression. See Table 3.2 for details. *Cov* = Covariate.

Cov	Mix SR	Mix Rate	Fire	Cov	SR x Cov	Rate x Cov	Fire x Cov	Delta AICc	df	weight	R^2
None	5.91***	-3.36*	-	-	3.65**	-	-	0	5	0.59	0.48
Age	4.14**	-3.80**	-	-2.72*	-	-	-	2.6	5	0.16	0.43
CV Biomass	4.30**	-5.17**	-	-2.38	-	-	-	5.6	5	0.04	0.37
Biomass	4.60**	-4.57**	-	1.99	-	-	-	5.7	5	0.03	0.37
None	4.83**	-4.13**	-	-	-	-	-	5.8	4	0.03	0.33
Land PCA	5.25***	-3.99**	-	-1.85	-	-	-	6.1	5	0.03	0.36
Edge:Area	5.05***	-4.27**	-	1.78	-	-	-	6.1	5	0.03	0.36
Land Use	7.96***	-4.12*	-	2.96	-6.48*	2.69	-	7.6	7	0.01	0.42
Age	4.41**	-4.33**	-	-2.43+	-0.76	1.22	-	7.9	7	0.01	0.41
Land Use	4.73**	-3.42+	-	2.16	-	-	-	8.1	5	0.01	0.31
CV WHC	4.61**	-3.94**	-	-1.58	-	-	-	8.3	5	0.01	0.31
Veg Cover	4.81**	-4.07**	-	-5.39	-	-	-	8.5	5	0.01	0.30
Fire	4.59**	-3.93*	5.32	-	-	-	-	8.5	5	0.01	0.30
Soil PCA	4.84**	-4.16**	-	-1.65	-	-	-	8.7	5	0.01	0.30
Fire	4.83**	-4.46**	1.22	-	-2.60*	1.22	-	9.3	7	0.01	0.38
Age	-	-	-	-3.56*	-	-	-	9.7	3	0.005	0.18
Biomass	4.58**	-4.27**	-	2.36+	0.65	1.52	-	10.4	7	0.003	0.36
Edge:Area	5.86**	-5.24**	-	2.40+	2.55	-0.92	-	11.3	7	0.002	0.34
Land PCA	5.54**	-3.15+	-	-1.68	0.95	0.55	-	11.7	7	0.002	0.33
Veg Cover	4.11**	-3.29*	-	-1.23	2.68	0.78	-	11.7	7	0.002	0.33
CV Biomass	4.34**	-5.10**	-	-2.21	-0.59	0.30	-	12	7	0.001	0.32
None	-	-	2.47+	-	-	-	-	13.5	3	<0.001	0.07
CV WHC	-	-	2.50+	-0.16	-	-	5.71+	13.8	5	<0.001	0.16
CV WHC	4.65**	-3.88*	-	-0.83	2.04	-1.64	-	14	7	<0.001	0.27
Edge:Area	-	-	2.97*	2.00	-	-	-	14.1	4	<0.001	0.10
NULL	-	-	-	-	-	-	-	14.2	2	<0.001	0
Land Use	-	-	-	4.35	-	-	-	14.2	3	<0.001	0.05
Land PCA	-	-	2.85+	-1.80	-	-	-	14.5	4	<0.001	0.09
CV WHC	-	-	-	-4.06	-	-	-	14.6	3	<0.001	0.04
Soil PCA	4.66**	-4.20**	-	-0.01	-0.99	-0.23	-	14.9	7	<0.001	0.25
Biomass	-	-	-	1.73	-	-	-	15.2	3	<0.001	0.02
CV WHC	-	-	2.05	-2.88	-	-	-	15.2	4	<0.001	0.07
Land Use	-	-	1.89	2.87	-	-	-	15.3	4	<0.001	0.07
Biomass	-	-	2.15	1.13	-	-	-	15.6	4	<0.001	0.05
CV Biomass	-	-	-	-1.42	-	-	-	15.7	3	<0.001	0
Edge:Area	-	-	-	1.25	-	-	-	15.9	3	<0.001	0
Land PCA	-	-	-	-1.19	-	-	-	16	3	<0.001	0

Table S3.2. (cont'd)

Cov	Mix SR	Mix Rate	Fire	Cov	SR x Cov	Rate x Cov	Fire x Cov	Delta AICc	df	weight	R^2
CV Biomass	-	-	2.24	-0.73	-	-	-	16	4	<0.001	0.04
Edge:Area	-	-	3.52*	2.46	-	-	1.83	16.1	5	<0.001	0.1
Veg Cover	-	-	2.39	-0.36	-	-	-	16.2	4	<0.001	0.04
Soil PCA	-	-	2.45+	0.2	-	-	-	16.2	4	<0.001	0.03
Veg Cover	-	-	-	-0.85	-	-	-	16.3	3	<0.001	0
Land PCA	-	-	2.26	-1.24	-	-	1.68	16.6	5	<0.001	0.08
Soil PCA	-	-	-	0.36	-	-	-	16.6	3	<0.001	0
Veg Cover	-	-	2.16	-0.8	-	-	2.19	17.8	5	<0.001	0.04
Land Use	-	-	2.52	3.01	-	-	-1.46	17.9	5	<0.001	0.04
CV Biomass	-	-	2.31	-0.35	-	-	0.94	18.5	5	<0.001	0.02
Biomass	-	-	2.18	1.11	-	-	-0.11	18.5	5	<0.001	0.02
Soil PCA	-	-	2.37	0.12	-	-	0.29	19.1	5	<0.001	0

Table S3.3. Correlation coefficients among factors used to predict native richness. Pearson's r, except for land use, which is result of one-way ANOVA; *p<0.05, +p<0.10.

	Mix SR	Mix Rate	Fire	Edge: Area	Land PCA	Biomass	CV Biomass	Veg Cover	Soil PCA	CV whc	Age
Mix Rate	0.46*										
Fire	0.27	-0.18									
Edge: Area	-0.09	0.02	-0.25								
Land PCA	0.27	0.18	0.21	-0.29							
Biomass	0.21	0.27	0.28	0.26	0.24						
CV Biomass	-0.42*	-0.54*	-0.30	0.07	-0.18	-0.46*					
Veg Cover	0.03	0.11	-0.20	-0.04	0.20	0.18	-0.12				
Soil PCA	0.04	-0.08	0.07	0.16	-0.15	-0.14	0.36+	-0.43*			
CV whc	-0.17	0.12	-0.29	0.04	0.05	-0.05	0.24	0.06	0.21		
Age	-0.20	0.01	-0.04	-0.12	0.02	-0.36+	0.21	0.05	-0.06	0.06	
Land Use	-	< in row crop	> in row crop	-	-	-	-	< in row crop	-	-	-

Table S3.4. Variation in functional group composition of seed mixes.

	Non-leguminous Forbs	Leguminous Forbs	C3 Graminoids	C4 Graminoids
Minimum Richness	4	1	0	3
Maximum Richness	51	8	9	6
Median Richness	22	5	2	5
Proportion of Richness	0.62	0.15	0.07	0.16
Minimum mass of Seeds Sown (g/m^2)	0.003	0.001	0	0.392
Maximum mass of Seeds Sown (g/m^2)	0.473	0.126	0.252	0.785
Median mass of Seeds Sown (g/m^2)	0.286	0.061	0.123	0.549
Proportion of Seeds Sown (by mass)	0.25	0.06	0.12	0.57

Table S3.5. Correlation coefficients among seed mix composition factors used to predict native richness. Pearson's r, *p<0.05, +p<0.10. SR=species richness. Coefficients between SR and rate of same functional group in **bold**.

	Total Rate	C3 Rate	C4 Rate	Forb Rate	Legume Rate	Total SR	C3 SR	C4 SR	Forb SR	Legume SR
C3 Rate	0.43*									
C4 Rate	0.07	-0.48*								
Forb Rate	0.82*	0.37+	-0.40*							
Legume Rate	0.69*	0.35+	-0.33+	0.70*						
Total SR	**0.48***	0.73*	-0.38+	0.51*	0.20					
C3 SR	0.26	**0.53***	-0.63*	0.55*	0.14	0.76*				
C4 SR	0.22	0.60*	**-0.23**	0.14	0.20	0.66*	0.33+			
Forb SR	0.48*	0.70*	-0.30	**0.48***	0.13	0.99*	0.71*	0.65*		
Legume SR	0.53*	0.73*	-0.36+	0.48*	**0.51***	0.81*	0.51*	0.55*	0.77*	
Age	-0.25	-0.08	0.48*	-0.61*	-0.23	-0.26	-0.61*	0.20	-0.24	-0.04

Figure S3.1. Change in richness over time differs by species origin. a) Native species richness declines with restoration age (r = -0.50, p < 0.01), while exotic species richness does not (r = -0.21, p = 0.28); b) declines in native species richness are not driven strongly by either the sown (r = -0.31, p = 0.11) or non-sown (r = -0.34, p = 0.07) component.

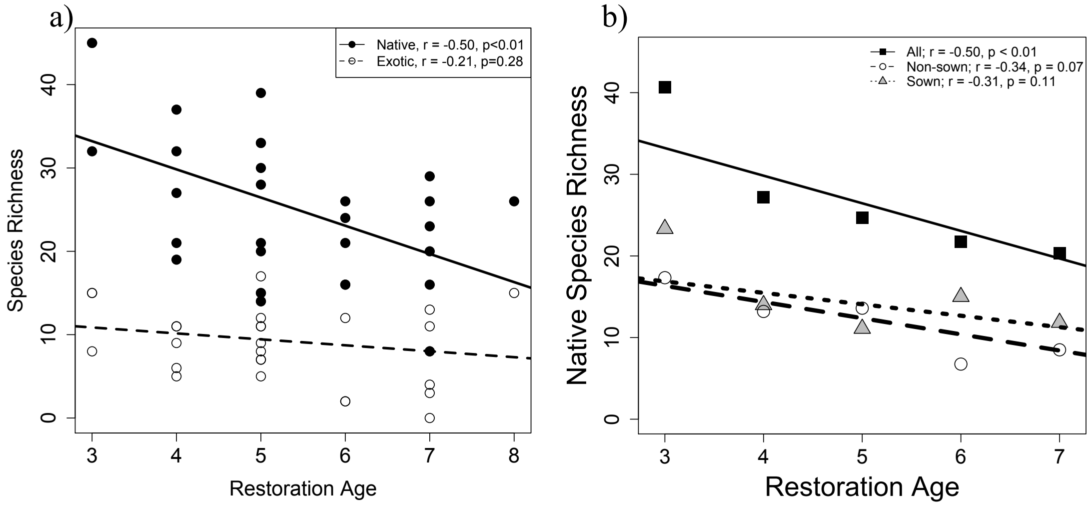


Figure S3.2. Interaction between seed mix richness and seeding rate not driven by legumes or C_4 grasses in seed mix. Heat map showing response of residuals from native SR~exotic SR regression to interactive effect of the seed mix richness and seeding rate of functional groups not shown in Figure 5, and between each functional group and the total richness and rate of seed mixes (see models in Table 3.3). Darker shading = higher proportional native richness (i.e., positive residuals from native SR ~ exotic SR regression); lighter shading = lower proportional native richness (i.e., negative residuals). Interactions between richness and seeding rate of legumes (a), and C_4 grasses (d); interactions between *total seed mix richness* and seeding rate of legumes (b) and C_4 grasses (e); interactions between *total seeding rate* and seed mix richness of legumes (c), C_4 grasses (f).

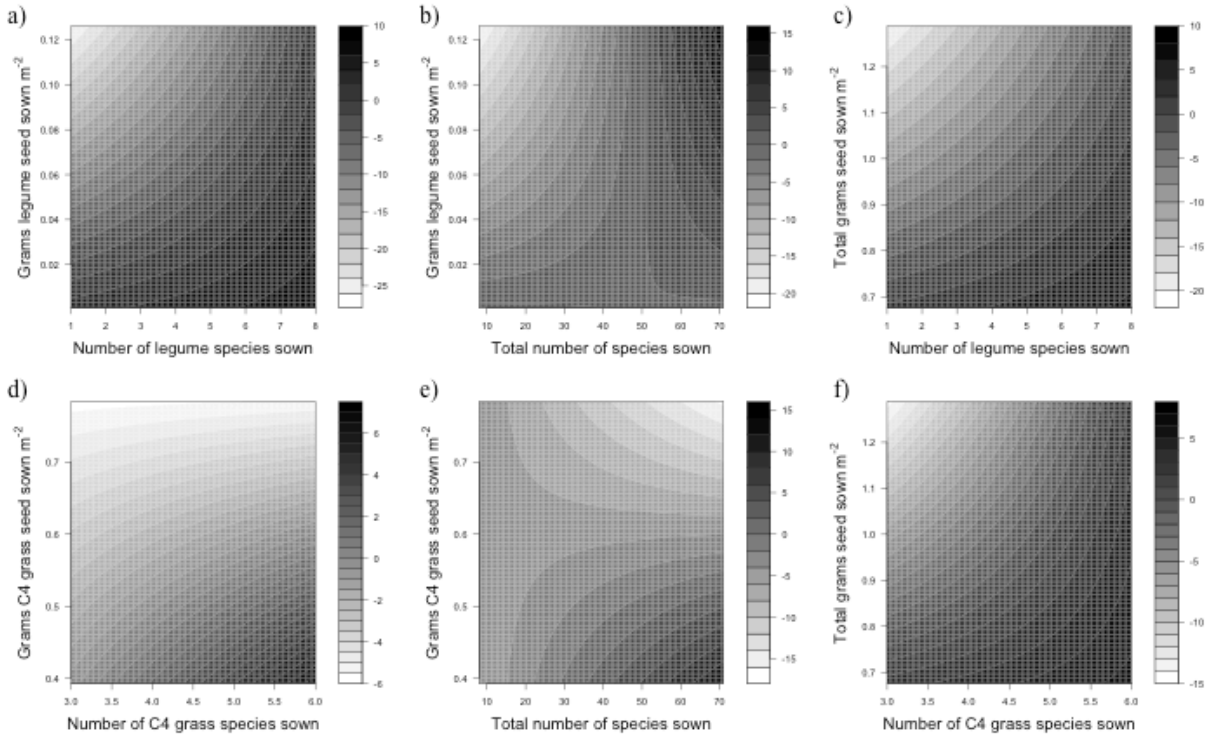


Figure S3.3. Dominant species effects differ across components of richness. The richness of exotic and non-sown native species is lower when *Andropogon gerardii* is abundant (a,d), while the richness of sown native species is associated instead with *Sorghastrum nutans* abundance (h). When controlling for the abundance of *A. gerardii* and *S. nutans*, the richness of exotic (c), non-sown native (f), and sown native species is not correlated with restoration age. Partial-residual plots for the model: richness~A. gerardii + S. nutans + age.

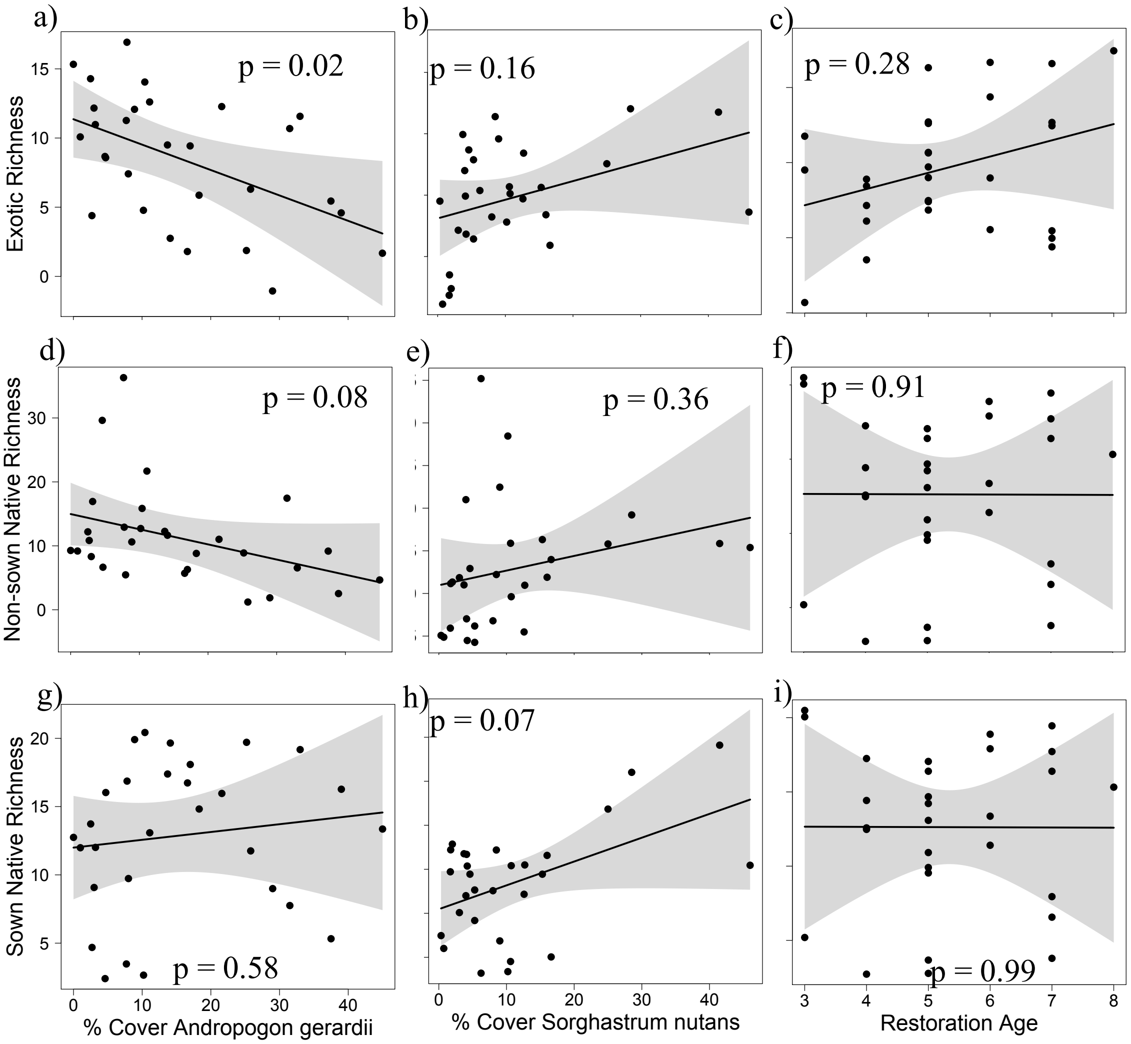


Figure S3.4. The restoration of native richness relative to exotic richness is linked to reduced exotic dominance. The relative abundance of exotic species was lower in sites where native richness was higher than predicted by the native-exotic richness relationship. Curve fit by logistic regression with a quasi-binomial error distribution; pseudo-$R^2 = 0.31$, $p<0.01$.

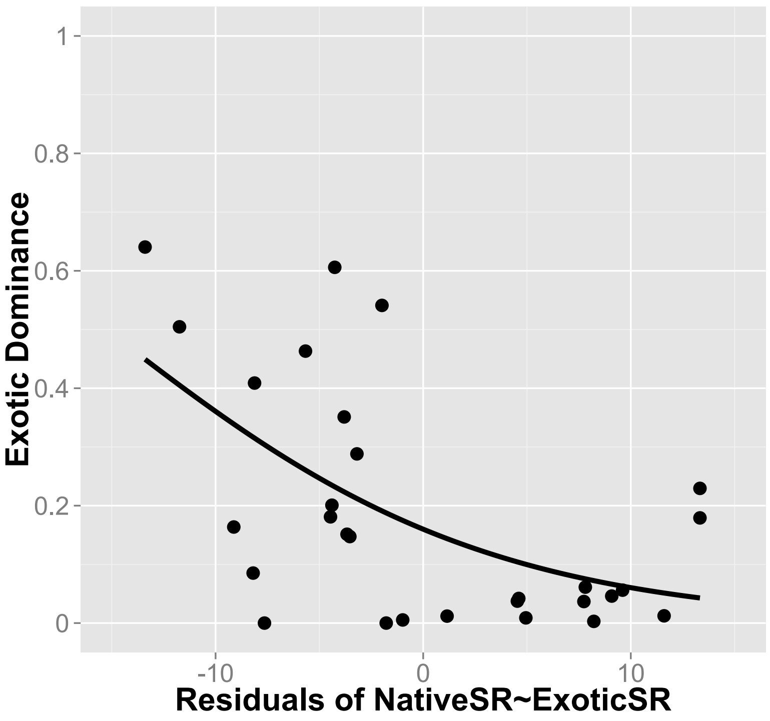


Figure S3.5. Random (null) vs. observed correlation coefficient and slope of native-exotic richness relationship. We used a randomization procedure to examine whether the observed native-exotic richness relationship differed from the null expectation. Here, the null expectation is the native-exotic richness relationship in communities randomly assembled from a regional species pool; without respect to species origin, and not shaped by native and exotic species responding similarly to factors like resource availability or heterogeneity (Stohlgren et al. 1999, Fridley et al. 2004). Holding the proportion of native and exotic species in the observed species pool constant, as well as the total site-level species richness, we generated a null distribution (with replacement) of both correlation coefficients (r) and slopes (s). We tested whether the observed r and s differed from the null distribution with one-tailed p-values. The observed pattern, however, did not differ from the null model based on communities simulated under the assumption of random assembly (correlation coefficient (r), one-tailed p = 0.28; slope, one-tailed p = 0.20).

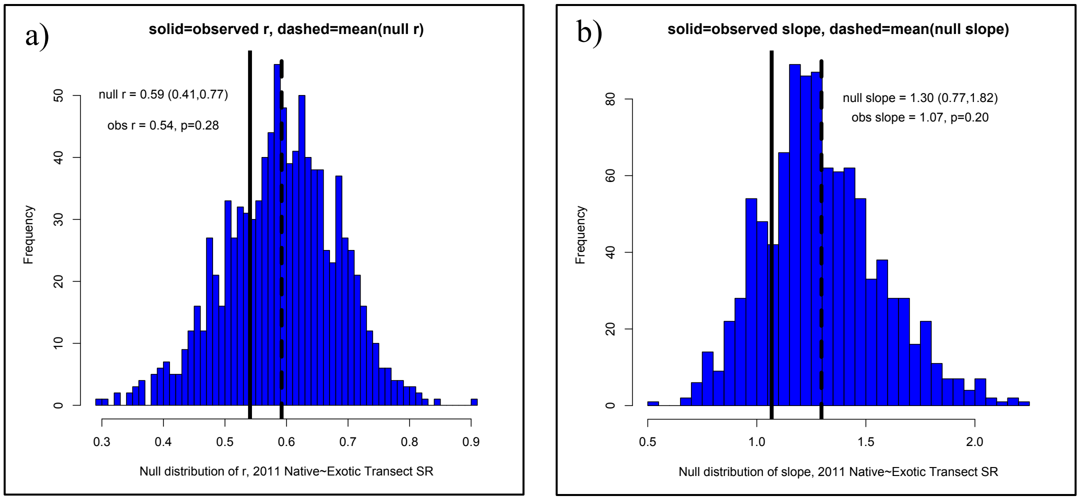
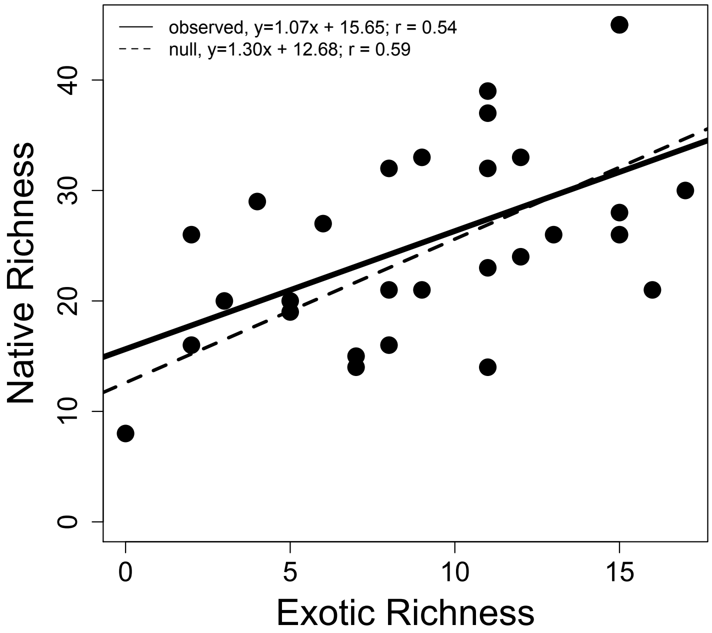


Figure S3.6. Observed native-exotic richness relationship does not differ from null. Observed = solid; null = dashed.



CHAPTER FOUR

RESTORING GRASSLANDS TO RESIST INVASION – RESTORED DIVERSITY CAN MEDIATE HISTORICAL LAND-USE EFFECTS

Abstract

While exotic species invasions are a primary threat to native ecosystems, the extent to which communities are invaded varies widely. This variation is due to processes occurring in the landscape surrounding invaded communities, as well as intrinsic community and ecosystem properties. However, the relative influence of these processes for controlling invasion remains poorly resolved. Importantly, this limits the capacity for developing management actions to promote invasion-resistant ecosystems. We used structural equation models to evaluate how factors influencing propagule pressure (landscape context and land-use history), abiotic site conditions (soil moisture availability), and the restored native community (richness of sown species, abundance of the community dominant *Andropogon gerardii*) related to the richness and abundance of invasive species in 29 tallgrass prairie grassland drestorations. We also tested whether management factors (seed mix richness and fire frequency) supported invasion resistance directly by reducing the richness or abundance of invasive species, or indirectly by modifying aspects of the restored community. We found that sandy, dry soils and *A. gerardii* abundance limited invasive richness, but propagule pressure and management did not. In contrast, invasive abundance was associated with management, propagule pressure, site conditions, and the restored native community. Invasive species abundances were dramatically lower in sites restored from row crops (1.6% cover) than in sites restored from hay fields or old fields (23.8% cover). Seed mix richness limited invasive species abundances indirectly by increasing the richness of sown species, which in turn was generally associated with lower abundances of invasive species. The abundance of *A. gerardii* also generally reduced invasive abundance. In contrast, fire frequency had virtually no direct or indirect effect on invasive richness or abundance. Our results illustrate how a suite of non-independent processes, including propagule pressure, resource availability, and community structure, can together affect the degree of invasion. From a practical perspective, land-use legacies may require management to reduce invasive species abundance (e.g., in seed banks) prior to restoration. However, managers can also mediate these effects and resist invasion by altering the restored community through seed additions.

Introduction

Exotic species invasions are one of the principal threats to populations and communities of native organisms, and often disrupt vital ecosystem functions (Parker et al. 1999, Vila et al. 2011). However, the extent to which communities are invaded varies widely, suggesting that some communities are better able to resist invasion than others. Theory attributes this variation to many factors (Catford et al. 2009), including propagule pressure of invaders (Simberloff 2009), resource availability and heterogeneity (Davis et al. 2000, Melbourne et al. 2007), and resident species diversity (Elton 1958, Levine et al. 2004). While there is empirical support for each of these hypotheses in some contexts, and most authors recognize that multiple factors may simultaneously drive invasion, the relative role of each process is unclear in most systems (Catford et al. 2009, Gurevitch et al. 2011).

The extent or degree of invasion, defined here as the abundance or richness of invasive species, is the outcome of processes occurring at multiple scales - both in the invaded community, and in the surrounding landscape (Lonsdale 1999, Richardson and Pysek 2006, Chytry et al. 2008, Catford et al. 2012, Guo et al. 2015). First, the propagule pressure of invaders from surrounding landscape - the rate, frequency, and diversity at which they arrive – drives initial population growth in the invaded community, and land use and landscape composition influence propagule pressure (Colautti et al. 2006, Simberloff 2009, Hufbauer et al. 2013). Landscapes with more intense anthropogenic disturbance (e.g., agricultural and urban development) support a greater density of species with traits linked to invasiveness, so anthropogenic disturbance is frequently correlated with propagule pressure (Stohlgren et al. 2006, Vila and Ibanez 2011, Gifford and Otfinowski 2013). Propagule pressure may also have a temporal component – variation in anthropogenic disturbances through time may determine the accumulation of invasive propagules in seed- and budbanks, especially on sites with agricultural histories (Gioria et al. 2014, Zylka et al. 2016). Second, both abiotic site conditions and aspects of the restored community determine the susceptibility of a community to invasion (Davis et al. 2000, Melbourne et al. 2007). Sites with low or homogenous resource availability are predicted to be more resistant to invasion, because fewer niches are available to be exploited (Davis et al. 2000, Shea and Chesson 2002, Melbourne et al. 2007). Similarly, communities with high diversity or where highly competitive species occur at high abundances are predicted to be more resistant to invasion (in part because less resources are available for invaders to exploit) (Davis et al. 2000, Kennedy et al. 2002, Smith et al. 2004). Third, additional factors may influence the degree of invasion indirectly, particularly by modifying community structure. Disturbances in particular can influence invasion resistance by modifying resource availability, altering community structure, or both (Burke and Grime 1996, Clark and Johnston 2011). For example, fire may have direct negative effects on some invasive species, or the effect of fire may be mediated via effects on native plant abundance (Copeland 2002, Howe 2011).

In this paper, we focus on how invasion ecology theory can be tested in restored ecosystems that vary in characteristics that are potentially important to invasion, including landscape context, land-use history, soil moisture, and diversity and abundance of the restored community. Furthermore, by testing this theory in real restorations, this theory can be translated into management guidelines. First, although it may be difficult to control propagule pressure, identifying how historical and surrounding land-uses influence invasion can inform site selection for restoration projects or allow managers to budget for more intensive invasive species control or for setting manager's expectations. Second, an understanding of how resource availability is linked to the degree of invasion, as with determinants of propagule pressure, can also inform site selection and planning (Zefferman et al. 2015). Third, managers can build invasion resistance into restored communities in multiple ways. For example, sowing more species at higher rates may resist invasion indirectly by restoring diverse communities of native species that will compete more efficiently for resources (Biondini 2007, Piper et al. 2007, Middleton et al. 2010). On the other hand, managers can restore natural disturbance regimes like fire that may directly reduce the degree of invasion (Howe 1994). Alternately, managers can manipulate the dominance of strong resource competitors (Smith et al. 2004) through natural disturbance regimes such as fire (Copeland 2002, Howe 2011). We use structural equation modeling to test how propagule pressure, site conditions, and community structure were linked to the degree of invasion in 29 tallgrass prairie grassland restorations, and to better understand how management can strengthen invasion resistance. Our purpose was twofold: provide a real-world test of theory, and assess the utility of this theory for guiding the management of invasive species in prairie restorations. In order to strengthen the applied value of our work, we classified invasive species narrowly, as the introduced species that have large negative impacts on native plants and communities and that are prioritized for control by managers. Specifically, we asked how management factors, seed mix richness and the frequency of prescribed fire, influenced the richness and abundance of invasive species and compared the relative influence of management to other factors that theory has linked to invasion success – landscape context, land-use history, soil moisture, and diversity and dominance in the sown community - as well as how management may influence the degree of invasion indirectly by modifying diversity and dominance.

Methods

Prairie establishment

We conducted our study in 29 tallgrass prairies in southwest Michigan, restored from former agricultural land, using methods typical for prairie restoration in the upper Midwest (Packard and Mutel 1997). Between 2003 and 2008, each site was cleared of existing vegetation with herbicides, and then sown with a mix of native prairie species. Following restoration, all sites were initially managed with mowing to minimize the fecundity of weeds and increase light availability for establishing native species. Thereafter, most restorations were managed with prescribed fire, to discourage woody species and exotic C^3 grasses and encourage sown native species. Additional site details are found below (*Classifying propagule pressure, abiotic site conditions, restored community and management*), and in Grman et al. (2014).

Field sampling

To characterize both the richness and abundance of invasive species (i.e., degree of invasion) and sown species (e.g. elements of community structure predicted to resist invasion), we sampled plant community composition in July-September 2011. We recorded the percent cover of all vascular plant species in 10 evenly spaced 1-m^2 plots along a 45-meter transect, located at the center of each site. The cover of all species could sum to greater than 100%. To quantify resources as a determinant of community invasibility, we sampled 80 soil cores per site (8 equidistant cores, 20 cm x 3 cm^2, around each 1-m^2 plot). We pooled soil samples by site, and analyzed soil organic matter, soil texture (sand, silt, and clay content), Mehlich-III phosphorus, Bray-II phosphorus, and pH (Brookside Laboratories, New Knoxville, OH, USA). We also determined plot-scale soil water holding capacity in the lab as the proportion of saturated wet to oven dry weight (after Brudvig and Damschen 2011).

Classifying invasive species

We classified all introduced plant species in our dataset as invasive or non-invasive with the U.S. Invasive Species Impact Rank (I-Rank, Morse et al. 2004). Here, invasive species are those introduced species that have large negative impacts on native plants and communities, and are also the species that are prioritized for control by managers. Because introduced species impacts may increase with time since introduction (Ahern et al. 2010), we conducted a parallel analysis with all introduced species, but the results were qualitatively similar (see Figure S4.3). The impacts of most species are not consistent in all habitats and regions of the United States, so we also crosschecked several regional published lists. We identified a core list of fourteen invasive species, which had I-Ranks associated with “Medium” or “High” impacts and occurred on at least two regional lists (Category A in Table S4.1). Finally, we consulted regional restoration professionals on the impacts of the remainder of introduced species. In so doing, we identified five additional species that are considered invasive, specifically in prairie restoration (Category B in Table S4.1), resulting in 19 invasive species included in our dataset. Next, we characterized the degree of invasion in two ways – richness as the cumulative number of invasive species per transect, and abundance as the mean percent cover of invasive species per m^2 along each transect. We interpreted invasive richness as an indicator of colonization success and an increased probability of future impacts. The percent cover of invasive species is a better determinant of current impacts. Finally, the response of individual species or groups of species may differ, and management can be tailored to address these species, so we also modeled the percent cover of the C^3 clonal grass *Poa pratensis*, all invasive *Trifolium* spp. (*T. hybridum*, *T. pratense*, and *T. repens*), and the summed cover of all invasive forbs. These species groups represent three different functional groups (C^3 grasses, legumes, forbs) that may respond differently to environmental conditions and management actions (Symstad 2000), and for which there was sufficient variation in abundances to satisfy the parametric assumptions of SEM. Percent cover values of invasive species groups were log-transformed to conform to assumptions of normality.

Classifying propagule pressure, abiotic site conditions, restored community and management

We characterized attributes of each site related to propagule pressure, including the landscape context and land use history of each restoration (Table 4.1). In ArcGIS, we calculated the area of forest, grassland, wetlands, agriculture, and development within 500 meters of the center of each site. To make inferences on the effects of landscape context using these highly correlated data, we conducted a principal components analysis on landscape data and used the first axis for analysis (hereafter, landscape context). Explaining 59% of the variation, high values on the landscape PC axis correspond to high cover of agriculture and low cover of forest and grassland. We consulted land managers on the land use prior to restoration. While all sites were

Table 4.1. Potential drivers that are hypothesized to determine the degree of invasion. Each hypothesized driver is linked to restoration based on theory (*How is theory applied to restoration?*), and based on how managers can manipulate each driver to reduce the degree of invasion (*Implications for management*). See Figure S4.1 for SEM meta-model.

	Hypothesis	**How is theory applied in restoration?**	**Implications for management**
Propagule Pressure			
Landscape Context (Landscape PC Axis)	Propagule pressure (Lonsdale 1999, Colautti et al. 2006, Simberloff 2009)	Some land cover types (e.g., agriculture) may support smaller invasive species populations than others (e.g., forest, grassland) and therefore contribute invasive propagules at lower rates.	**Site selection**. Managers can select sites in landscapes with lower propagule pressure, or plan/budget to engage in more intensive management, post-restoration.
Land-use History	Propagule pressure (Lonsdale 1999, Colautti et al. 2006, Simberloff 2009)	Differences in historical land management (row crops vs. perennial grasslands) select for different types and abundances of invasive species in the seedbank and budbank.	**Site selection/Pre-restoration management**. Managers can select sites with histories that contribute lower propagule pressure; or adjust management prior to restoration to reduce propagule pressure.
Resource Availability			
Soil Moisture (Soil PC Axis)	Fluctuating resources (Davis et al. 2000); Invasion windows (Shea and Chesson 2002)	Sites with lower resource availability (here, primarily soil moisture, a key driver of community dynamics in grassland) are more difficult to invade.	**Site selection/Post-restoration management**. Managers can select sites with lower resource availability; or plan/budget to engage in more intensive management, post-restoration.
Community Structure			
Sown Richness (Established)	Diversity-invasibility (Elton 1958, Levine et al. 2004)	The establishment of a diverse community of sown native species confers biotic resistance; diverse communities of resident species occupy available resources more efficiently (e.g., complementarity).	**Seed additions.** Managers can sow more diverse seed mixes.
% cover of dominant species (*A. gerardii)*	Selection effect (Crawley et al. 1999, Smith et al. 2004)	Sites dominated by a single highly competitive species may be more resistant to invasion; *A. gerardii* may draw down resources more effectively than a diverse community.	**Seed additions/Prescribed fire.** Managers can sow *A. gerardii* at higher rates, or adjust timing of burns to encourage *A. gerardii*.
Management			
Seed Mix Richness (Sown)	Diversity-invasibility (Elton 1958, Levine et al. 2004)	Sowing more species should establish a more diverse "resident community" and increase biotic resistance to invasive species.	**Seed additions.** Managers can sow more diverse seed mixes.
Fire Frequency	Disturbance (Hobbs and Huenneke 1992)	Fire increases light availability but decreases soil nutrient availability, so may increase or decrease invasibility. The response of individual species to fire also varies - so the response of specific invaders may vary.	**Prescribed fire.** Managers can adjust the timing of burns.

historically in row crops, sites occupied different land uses immediately prior to restoration – perennial grasslands (hay fields, old fields, pastures; n=16) and row crops (n=13). Landscapes and land uses dominated by non-agricultural land uses, especially perennial grasslands, are more likely to accumulate larger populations of invasive species (Gifford and Otfinowski 2013). We predict that these landscapes and land uses will be associated with increased propagule pressure (Lonsdale 1999, Simberloff 2009) (Table 4.1).

We also characterized abiotic site conditions and the community structure of sown species (Table 4.1). First, we conducted a principal components analysis on site-level soils data. The first axis, which we used as a measure of resource availability, explained 56% of the variation in soil resources. High values on this axis (hereafter, soil moisture) correspond to sandy sites with low water holding capacity. Sandy, dry sites represent low overall resource availability and provide shorter windows of opportunity for invasive species establishment by retaining moisture for shorter periods of time (Shea and Chesson 2002) (Table 4.1). Second, we used the richness of sown species and the percent cover of the dominant sown species, *Andropogon gerardii* as aspects of community structure that may confer invasion resistance. We used sown richness, calculated as the cumulative richness of sown species that were observed along each transect, as a measure of resident community diversity (Levine and D'Antonio 2004) (Table 4.1). *Andropogon gerardii*, the most abundant C^4 grass at our sites, is a widespread dominant across a wide variety of soils in both remnant and restored prairies (Weaver and Fitzpatrick 1932, Carter and Blair 2012). Dominance of C^4 grasses, rather than species richness, often drives invasion resistance by competing more efficiently for resources (Tilman 1999, Smith et al. 2004, Mahaney et al. 2015) (Table 4.1).

Additionally, we used seed mix richness and prescribed fire frequency to test for the effects of management on the degree of invasion (Table 4.1). We obtained data on seed mix richness from the restoration contractor (Native Connections, Three Rivers, MI). Sites were sown with 8-71 species (mean = 35 species). Increasing seed mix richness should establish a more diverse resident (e.g. sown) community (Grman et al. 2013), which may more effectively resist invasion (Table 4.1). Fire is a primary natural disturbance in our system, and more frequent fire may directly limit the richness and abundance of invasive species (Emery and Gross 2005, Brudvig et al. 2007, Li et al. 2013). We consulted land managers on the prescribed fire history of each site. Sites were burned between 0 and 4 times since being restored, and we calculated fire frequency as the number of burns divided by years since restoration. While more frequent fire may reduce invasive species such as C^3 grasses without impacting C^4 grasses (Li et al. 2013), more frequent fire may also resist invasion indirectly by increasing the cover of *A. gerardii* (Copeland 2002, Howe 2011) (Table 4.1).

Data analysis

We constructed structural equation models (SEM; Grace 2006) to test how propagule pressure, site conditions, and community structure influence invasion and how management might influence these processes. We used a SEM approach to better understand both direct and indirect causal relationships that lead to observed levels of invasion, as a test of theory and in order to better inform management (Grace et al. 2010). The exact metric used to characterize the degree of invasion can have different interpretations (Guo et al. 2015), and we created five separate models with different invasion-related endogenous variable – invasive richness, the summed percent cover of all invasive species, and the percent cover of specific invasive species or groups (*Poa pratensis*, *Trifolium* spp., and all invasive forbs).

We started by fitting the same simple SEM for each invasion metric. This initial model included the direct effects of invasive propagule pressure from the surrounding landscape (landscape PC axis) and via site history (land use history), abiotic site conditions (soil moisture), community structure (richness of established sown species, abundance of *Andropogon gerardii*), and management (prescribed fire frequency) (Figure S4.1). We also modeled the indirect effect of management on invasion through its effects on community structure, by including an effect of seed mix richness on the sown species richness, and the effect of fire frequency on the abundance of *A. gerardii*. Then, we assessed change in model fit (primarily by likelihood ratio tests), after adding paths suggested by modification indices. When we determined a final model, we calculated standardized path coefficients (r) for each predictor. Finally, to estimate the influence of each variable on invasive richness and abundance, we calculated the total standardized effect (TSE) of each predictor: the sum of all indirect and direct standardized path coefficients.

Results

Modification indices suggested that soil moisture also influenced the richness of sown species. We therefore included this path in our models, and this improved the fit of models for both richness (model $\chi^2 = 12.53$, df=9, $p = 0.19$) and cover (model $\chi^2 = 11.16$, df=9, $p = 0.27$). These models explained 46% of the variation in the richness, and 78% of the variation in the cover of invasive species. Models with the same structure predicted 45% of the variation in the cover of the invasive C^3 grass *Poa pratensis* ($\chi^2 = 11.14$, df=9, $p = 0.27$), 68% of *Trifolium* spp. cover ($\chi^2 = 11.50$, df=9, $p = 0.24$), and 32% of summed invasive forb cover ($\chi^2 = 17.76$, df=9, $p = 0.23$). In all cases, the models fit the data well ($p > 0.05$ indicates good fit; see Table S4.2 for additional fit measures).

Invasive species richness was strongly associated with abiotic site conditions and community structure (Figures 4.1a, 4.2a), while propagule pressure, site conditions, community structure and management all influenced invasive species cover (Figures 4.1b, 4.2b). Invasive

Figure 4.1. Structural equation models for invasive richness (a) and percent cover (b). Solid arrows = positive effect, dashed = negative; black arrows = significant effect ($p<0.05$); gray = non-significant ($p>0.05$). Width of arrows roughly proportional to effect size: predictions for each path in Table 4.1; standardized path coefficients in Table 4.2.

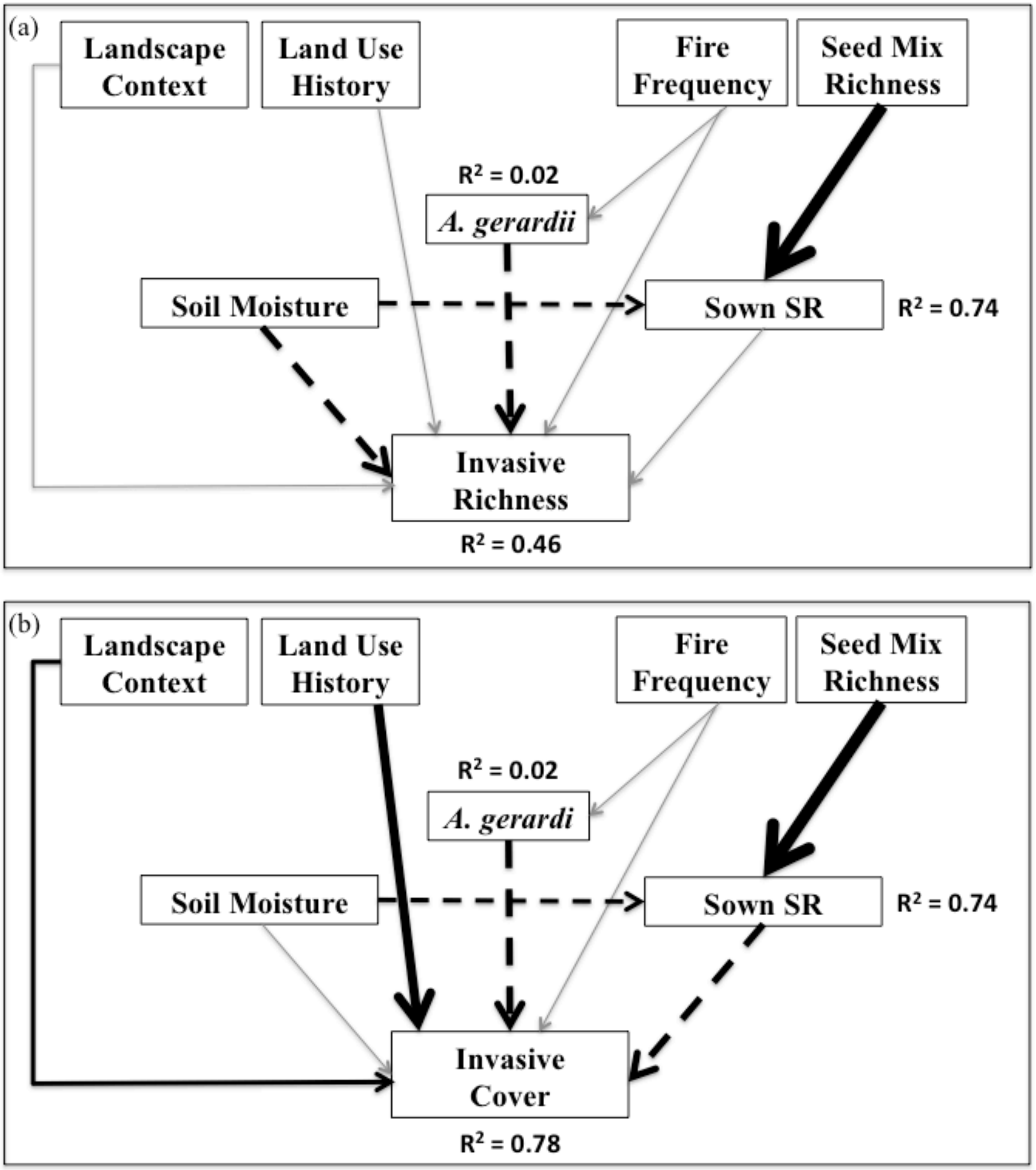
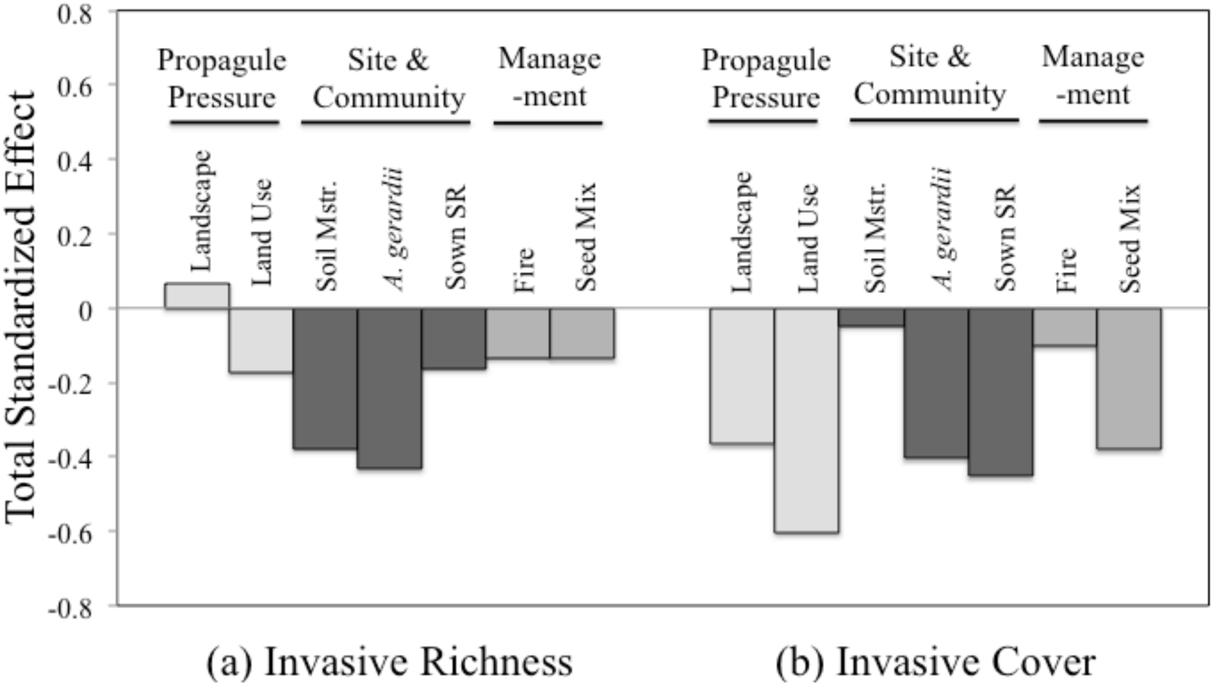


Figure 4.2. Total standardized effects on invasive richness (a) and cover (b). Effects of landscape context (landscape), land use history (land use), soil moisture (soil mstr.), abundance of *Andropogon gerardii* (*A. gerardii*), richness of sown speices (sown SR), seed mix richness (seed mix), and fire frequency (fire). See Table 4.2 for parameter estimates.



richness was lower in in sites dominated by *Andropogon gerardii* (r = -0.43, p < 0.001; Table 4.2), and in sandy sites with lower soil moisture retention capacity (r = -0.42, p < 0.001; TSE = -0.38; Table 4.2). The effects of both seed mix richness (TSE = -0.14) and fire frequency (TSE = -0.13) on invasive species richness were weak (Table 4.2), suggesting a limited role for these management practices in determining invasive richness. Invasive species cover was reduced by sown species richness (r = -0.45, p < 0.001; Table 4.2) and *A. gerardii* abundance (r = -0.41, p < 0.001; Table 4.2), and was lowest in sites that were in row crops immediately prior to restoration (r = -0.60, p < 0.001; Table 4.2). Soil moisture only had a marginally significant direct effect on invasive cover (r = -0.15, p = 0.099; Table 4.2), but also indirectly increased invasive cover by reducing sown species richness (r = -0.22, p = 0.02; Table 4.2), resulting in no overall effect of soil moisture on invasive cover (TSE = -0.05; Table 4.2). Fire frequency had no direct or overall effect on invasive cover (TSE = 0.01) (Table 4.2). Seed mix richness, however, had a negative effect on invasive cover (TSE = -0.26) by increasing sown species richness (r = 0.84, p < 0.001; Table 4.2). The response of invasive species groups to land-use history and *A. gerardii* mirrored the response of total invasive cover, but otherwise varied among species. As we found for summed invasive species cover, sites recently in row crops had or trended toward lower cover for *Poa pratensis* (r = -0.40, p < 0.001), *Trifolium* (r = -0.22, p = 0.07), and invasive forbs (r = -0.39, p = 0.03) (Table 4.2; Figures 4.3, 4.5); and *A. gerardii* abundance limited or tended to limit the cover of *Poa pratensis* (r = -0.27, p = 0.06) and *Trifolium* (r = -0.50, p < 0.0001) (Table 4.2; Figures 4.2, 4.4). *Poa pratensis* was also less abundant in landscapes dominated by agriculture (r = -0.40, p < 0.01), while *Trifolium* spp. were limited by soil moisture (r = -0.44, p < 0.0001; TSE = -0.50). Sown species richness was associated with reduced invasive forb cover (r = -0.36, p = 0.03), and increased *Trifolium* spp. cover (r = 0.27, p = 0.02), but did not influence *P. pratensis* (r = -0.23, p = 0.15). Because seed mix richness increased sown species richness (r = 0.84, p < 0.001; Table 2), seed mix richness was associated with higher cover of *Trifolium* spp. (TSE = 0.22), and lower cover of invasive forbs (TSE = -0.31) and *P. pratensis* (TSE = -0.20).

Discussion

We tested the relative roles of multiple factors hypothesized to influence invasion, and used that theory to ask how managers might manipulate community structure to better resist exotic species invasions in prairie restorations. As predicted, each class of drivers we considered

Figure 4.3. Structural equation models for percent cover of invasive species groups. *Poa pratensis* (a), *Trifolium* spp. (b), and all invasive forbs (c). Solid arrows = positive effect, dashed = negative; black arrows = significant effect ($p<0.05$); gray = non-significant ($p>0.05$). Width of arrows roughly proportional to effect size: predictions for each path in Table 4.1; standardized path coefficients in Table 4.2.

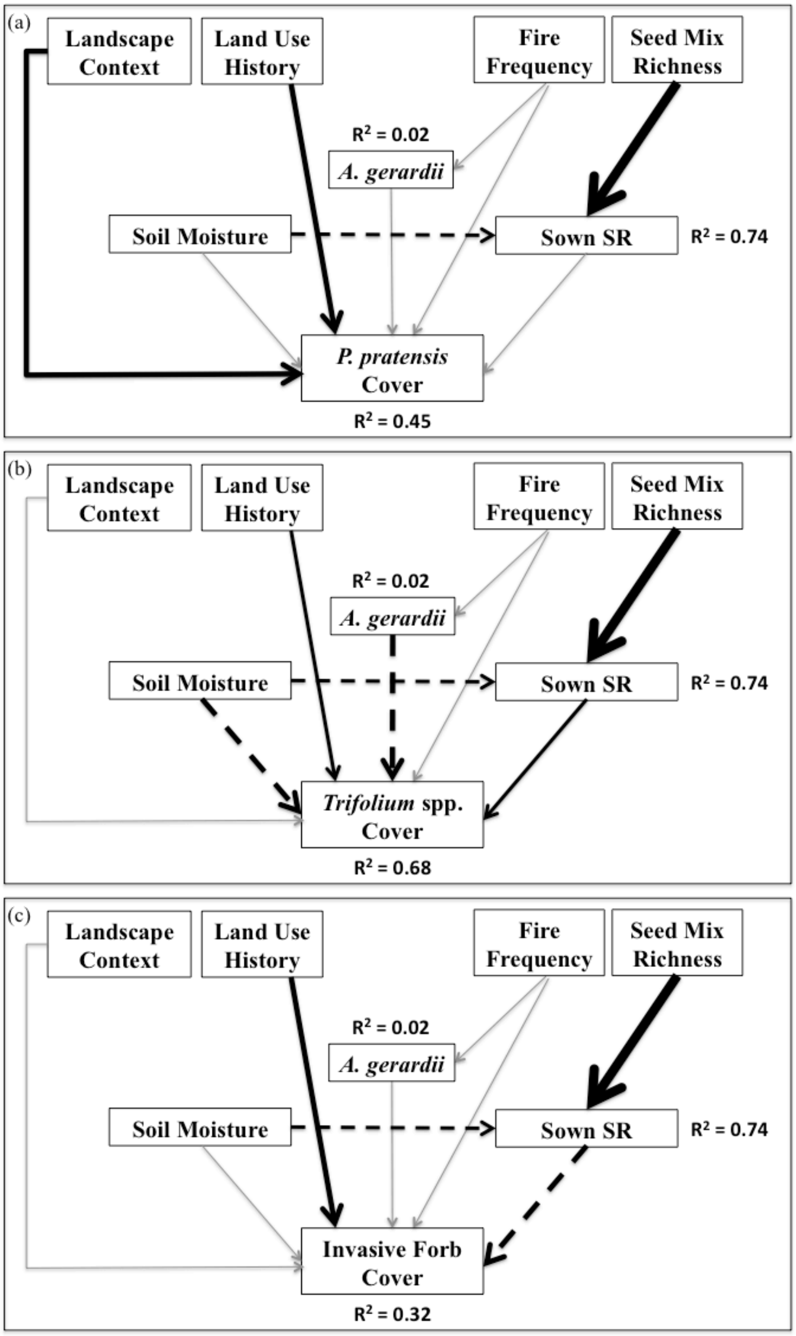
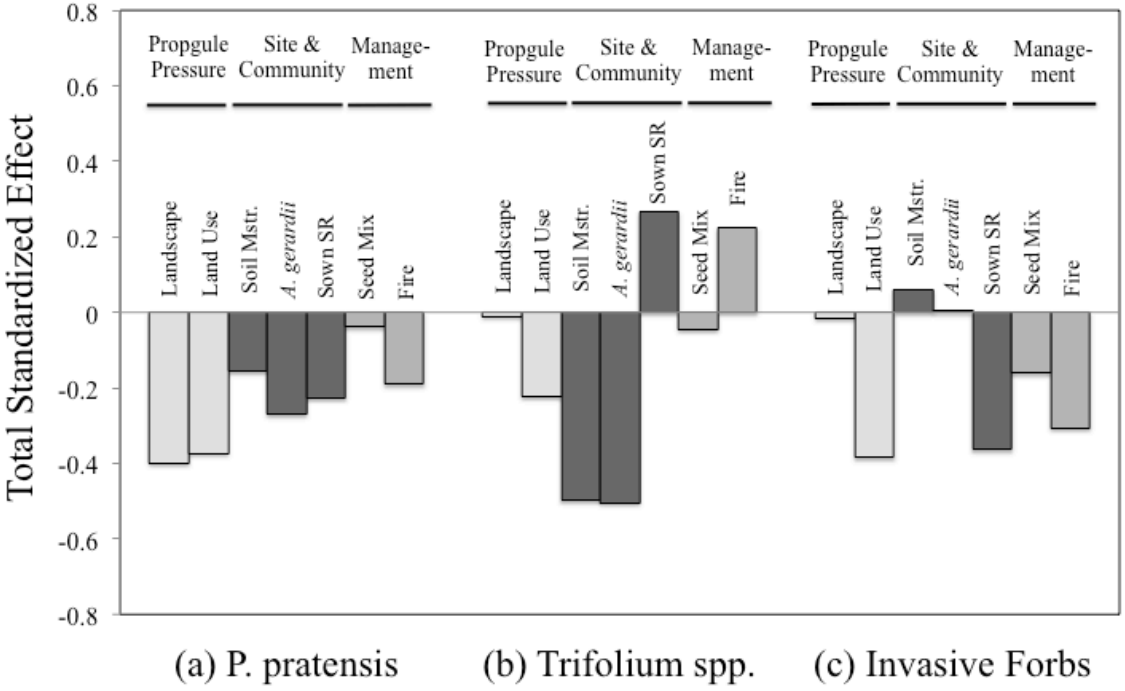


Figure 4.4. Total standardized effects on *Poa pratensis* (a), *Trifolium* spp. (b), and all invasive forbs (c). Landscape context (landscape), land use history (land use), soil moisture (soil mstr.), abundance of *Andropogon gerardii* (*A. gerardii*), richness of sown speices (sown SR), seed mix richness (seed mix), and fire frequency (fire). See Table 4.2 for parameter estimates.



– propagule pressure, abiotic site conditions, community structure, and management – explained variation in the degree of invasion. Invasive species richness was limited most strongly by site conditions and community structure and not management. In contrast, management limited invasive species abundances by increasing invasion resistance of the sown community. However propagule pressure also strongly influenced invasive abundance, particularly via land-use history. Among factors predicted to drive the degree of invasion, community structure (specifically, the abundance of *A. gerardii*) was consistently associated with invasion resistance, while site conditions (soil moisture) and propagule pressure (land-use history) appeared to play particularly strong roles in driving the richness and abundance of invasive species, respectively.

Below, we discuss how the different invasion hypotheses contributed to invasion in our study, beginning with factors that are difficult to control (propagule pressure, abiotic site conditions), and ending with factors that can be addressed through management.

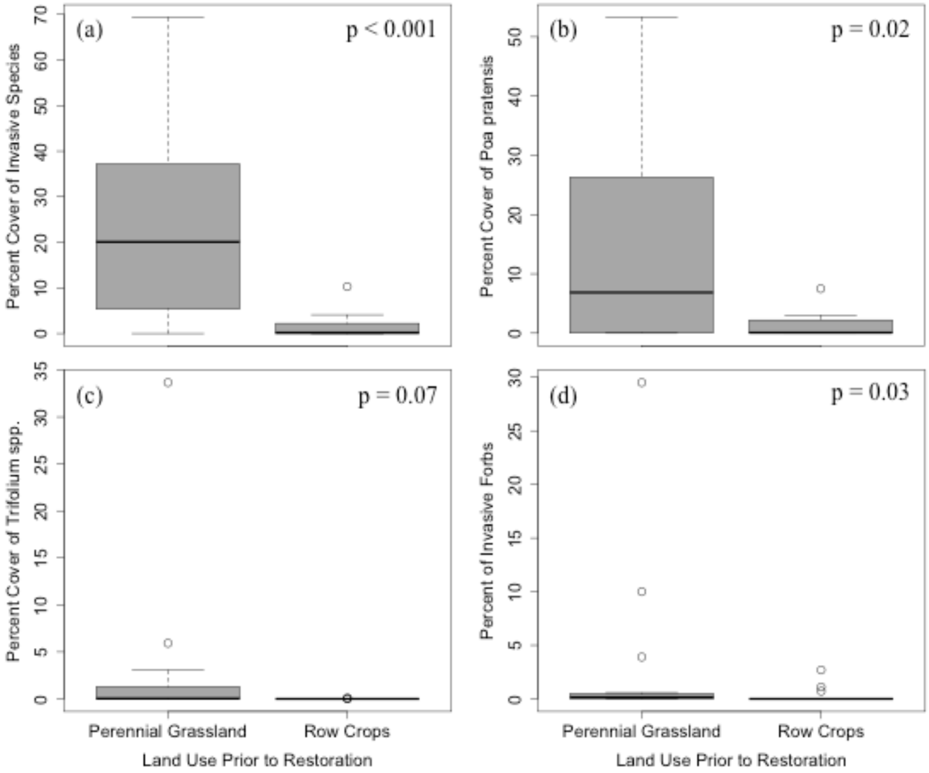
Impacts of propagule pressure - landscape context and land use history

Invasive species abundances were higher in sites restored from perennial grasslands, and to a lesser degree, in landscapes dominated by perennial grassland and forest instead of agriculture. Propagule pressure drives invasion by overcoming demographic barriers to colonization by increasing the density, frequency, and richness of propagules immigrating into a community (Simberloff 2009, Hufbauer et al. 2013). Invasive species develop larger populations over time in perennial habitats (i.e., in the absence of frequent or recent disturbance such as tillage) such as hay- and old fields. Despite attempts to eliminate them prior to restoration, large

Table 4.2. Effects of each exogenous variable each endogenous variable in SEMs. Effects on: sown SR (species richness), *Andropogon gerardii*, inv (invasive) SR, inv cover, *Poa pratensis* cover, *Trifolium* spp. cover, and inv forb cover. Including direct standardized path coefficients (***p < 0.001, **p < 0.01, *p < 0.05, +p < 0.10), and total standardized effect (**TSE**); from structural equation models in Figures 4.1 and 4.3.

	Sown SR	*A. gerardii*	Inv SR	**TSE**	Inv Cover	**TSE**	*P. pratensis*	**TSE**	*Trifolium*	**TSE**	Inv Forbs	TSE
Land PCA	-	-	0.07	**0.07**	-0.37***	**-0.37**	-0.40**	**-0.40**	-0.01	**-0.01**	-0.02	**-0.02**
Land Use	-	-	-0.17	**-0.17**	-0.60***	**-0.60**	-0.37*	**-0.37**	-0.22+	**-0.22**	-0.39*	**-0.39**
Soil PCA	-0.22*	-	-0.42**	**-0.38**	-0.15+	**-0.05**	-0.21	**-0.16**	-0.44***	**-0.50**	-0.02	**0.06**
A. gerardii	-	-	-0.43**	**-0.43**	-0.41***	**-0.41**	-0.27+	**-0.27**	-0.50***	**-0.50**	0.01	**0.01**
Sown SR	-	-	-0.16	**-0.16**	-0.45***	**-0.45**	-0.23	**-0.23**	0.27*	**0.27**	-0.36*	**-0.36**
Fire Freq.	-	-0.14	-0.19	**-0.13**	-0.16	**-0.10**	-0.08	**-0.04**	-0.11	**-0.04**	-0.16	**-0.16**
Mix SR	0.84***	-	-	**-0.14**	-	**-0.38**	-	**-0.19**	-	**0.22**	-	**-0.31**

Figure 4.5. Invasive species cover is lower in sites restored from row crops than from perennial grasslands. (a) all invasive species, (b) the invasive C3 invasive grass *Poa pratensis*, (c) *Trifolium* spp., and (d) all invasive forbs.



seed- and budbanks remain in sites restored from perennial grasslands, from which these species quickly establish populations (Gioria et al. 2014, Zylka et al 2016). Invasive populations also appear to be augmented by dispersal from perennial habitats in the surrounding landscape, especially for the clonal C^3 grass *Poa pratensis,* which is likely to be generally abundant in post-agricultural landscapes (Toledo et al. 2014, Zylka et al 2016). Drivers related to propagule pressure did not influence invasive richness, suggesting that propagule pressure generally augmented existing invasive populations, as opposed to introducing additional invasive species.

Impacts of site conditions – soil moisture

Low soil moisture limited invasive richness and the abundance of *Trifolium* spp. Sandy soils with low water holding capacity represent lower overall resource levels and a harsher environment, provide shorter windows of opportunity for invasive species establishment by retaining moisture for shorter periods of time, and may constrain which species are able to persist at these sites (Shea and Chesson 2002, Zefferman et al. 2015). Interestingly, low soil moisture also limited sown richness, likely for similar reasons (Grman and Brudvig 2014). When sown richness reduced invasive cover (summed invasive cover and cover of invasive forbs), the indirect effect of soil moisture on invasive cover was largely neutral (or more weakly negative) because soil moisture reduced sown richness, thereby reducing the negative effects of sown richness on invasive cover. In contrast, the abundance of the invasive legume *Trifolium* spp. was positively correlated with sown richness. By reducing the richness of sown species, soil moisture therefore had an indirect negative effect on *Trifolium* spp. abundance.

Impacts of community structure – Andropogon gerardii *abundance and sown richness*

The richness and abundance of invasive species was lower in sites with high sown species richness, greater abundance of *Andropogon gerardii*, or both. Among invasive species groups, *A. gerardii* more strongly resisted the mat-forming *P. pratensis* and *Trifolium* spp., likely by limiting light and soil resource availability for invasive species to exploit during colonization and establishment (Tilman and Wedin 1991, Silletti et al. 2004, McCain et al. 2010). In contrast, sown richness had particularly strong negative effects on invasive forbs, presumably because the additional species found in sites with high sown richness occupied the same niche-space that invasive forbs would otherwise occupy (Funk et al. 2008). Greater sown species richness was likely associated with more complete utilization of multiple resources, which were subsequently unavailable for invaders to exploit (Kennedy et al. 2002, Levine and D'Antonio 2004). The direction of causality, that of sown richness limiting invasive species abundances, is model-implied and supported by theory and experiments (Levine and D'Antonio 2004). However, it is also possible that invasive species abundances instead limit sown richness, or the two are collinear along an unmeasured gradient.

Impacts of management – seed mix richness and prescribed fire

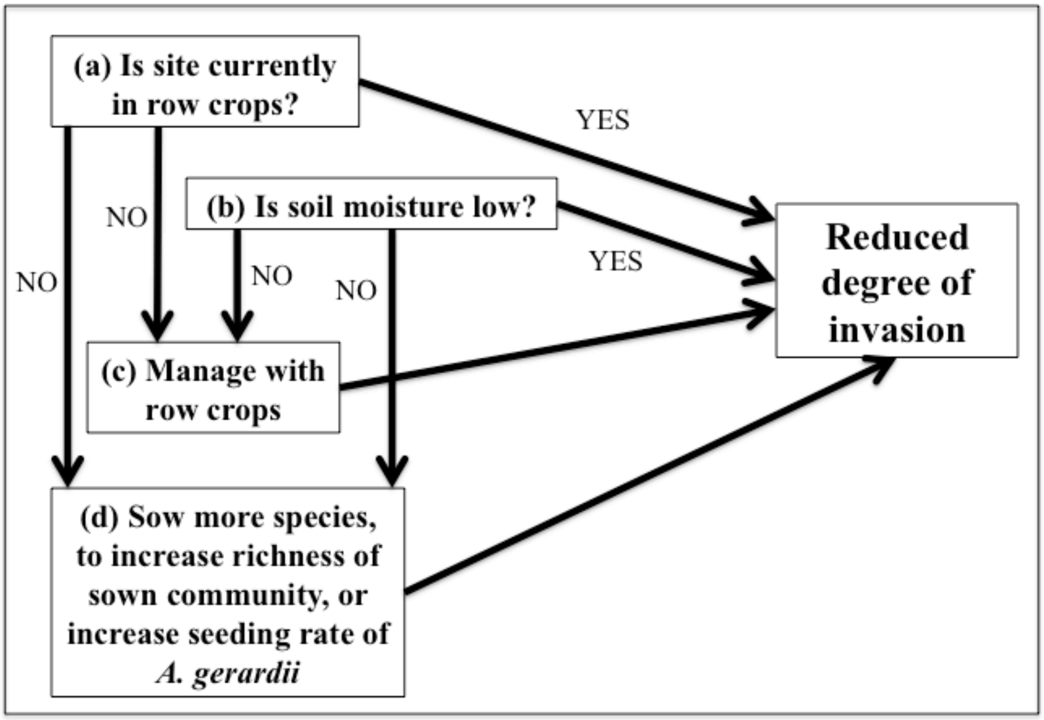
Sowing seed mixes with a greater number of prairie species encouraged the establishment of a more diverse resident community, which in turn conferred greater invasion resistance in the form of reduced cover of most invasive species. Therefore, managers can effectively manipulate the propagule pressure of native prairie species to partially resist the colonization and establishment of invasive species (Melbourne et al. 2007, Funk et al. 2008). In fact, dispersal via seed mixes is the strongest determinant of sown species richness (Grman et al. 2013), although dry, sandy soils limit sown species richness in our models here, and in previous work (Grman and Brudvig 2014). Prescribed fires, another major management tool, typically occur during early-spring green-up in order to target invasive C^3 grasses such as *P. pratensis*, which often serves to promote native C^4 grasses such as *A. gerardii* (Howe 1994). However, fire frequency had negligible effects on invasive richness and abundance in our models, as well as *A. gerardii* abundance. The impact of fire on invasive species may not be consistent across space, as fire effects often vary with seasonality (Howe 1994), soil type, and moisture availability (Collins 2000), and other factors that vary geographically (Bowles and Jones 2013).

Summary and management implications

By considering a suite of processes believed to influence the extent exotic species invasions, we were able to explain a considerable amount of the variation ($R^2 \geq 0.45$ in all but one model) in both the richness and abundance of invasive species. As predicted, propagule pressure, abiotic site conditions, and community structure all played a role in determining the degree of invasion. Our study supports many theoretical predictions, including: 1) communities with lower resource availability (Davis et al. 2000), greater resident species diversity (Levine et al. 2004), and higher abundances of superior competitors (Smith et al. 2004) are often less invasible; and 2) communities likely exposed to higher propagule pressure (particularly through seedbanks resulting from prior land uses) are more heavily invaded (Simberloff et al. 2009). With SEM, we too important steps toward clarifying the relative importance of each hypothesized invasion driver in our system, and how their effects varied among metrics used to define the degree of invasion. Community structure was a consistently important driver – the abundance of *A. gerardii* was strongly linked to both lower invasive richness and abundances. Soil moisture, on the other hand, was particularly important for limiting invasive richness, but not abundance; while land-use history had large effects on invasive abundance and not richness.

The SEM approach also allowed us to connect management actions (seed sowing, fire) to measurable invasion outcomes in sites undergoing restoration, in the context of realistic environmental variation. Direct management of invasive species, through manual and chemical means, is effective but time-consuming, and it is more efficient to build invasion resistance into restored communities (Suding 2011). In order to reduce the richness and abundance of invasive species in prairie restoration, our study suggests specific management actions during at least three phases of the restoration process – site selection, site preparation, and establishment of the

Figure 4.6. Decision tree for reducing degree of invasion in prairie restoration. Invasion may be limited in sites managed in row crops prior to restoration (a) and sites with low soil moisture (b). In other sites, the degree of invasion may be reduced by (c) managing with row crops for a year or two prior to restoration or by (d) increasing the richness of sown species or abundance of *Andropogon gerardii* via augmented seed additions.



restored community. Managers can directly control some factors that dictate the degree of invasion, while others may present inherent limitations to managing invasive species. First, sites with lower soil moisture availability are likely to have fewer invasive species overall, and lower abundances of some species in particular (e.g., *Trifolium*), although it can also be more challenging to establish desirable sown species in low moisture sites as well. Second, sites formerly in row crops, and in some cases sites in landscapes dominated by agriculture, are likely to have lower abundances of invasive species, especially clonal C^3 grasses (e.g., *Poa pratensis*).

For these reasons, selecting sites with lower soil moisture and row-crop land-use history may benefit restoration by resulting in less invasion and need for subsequent management to target invasive species (Figure 4.6a,b). Therefore, when restoring from row crops, and in drier sites, standard site preparation may be sufficient for reducing the degree of invasion. When restoring from sites in perennial vegetation and in clayey soils, it is advisable to take a more aggressive approach toward reducing existing vegetation prior to planting. In practical terms, that may translate into several herbicide treatments during a single year prior to planting, or multiple years of herbicide and other treatments (disking, planting to row crops such as soybeans) (Figure 4.6c). Finally, establishing a native plant community that naturally resists invasion, i.e. a resilient community, is a primary goal of restoration (Suding 2011), which may be especially beneficial in wetter sites restored from perennial grasslands (Figure 4.6d). Our analyses suggest that the degree of invasion is low in sown communities that are either high in species richness, or where *Andropogon gerardii* is abundant. Increasing the richness of the sown community is easily achieved by simply increasing the number of species sown (Grman et al. 2013). Increasing the abundance of *A. gerardii*, although typically not a challenge (or goal) in prairie restoration can similarly be achieved by sowing *A. gerardii* at high rates (Figure S4.2). However, abundance of *A. gerardii*, which had stronger and more consistent effects on invasion resistance, is generally achieved at the expense of diversity in general, including of native species (Dickson and Busby 2009, Carter and Blair 2012). Therefore, managers may need to balance between the priorities of stronger invasion resistance, via *A. gerardii* dominance; or establishing diverse sown communities with weaker invasion resistance. Some managers advocate a third, staged approach, whereby early dominance of *A. gerardii* is followed by auxiliary seed-sowing or other management to establish diverse communities of native prairie species.

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APPENDIX

Table S4.1 List of invasive species in dataset, and summary information on invasive and sown richness and cover. Lists: State/Province lists including or (- not including) species. Criteria: A=Core list; B= Identified by managers (see main text).

Site	*Agropyron repens*	*Alliaria petiolata*	*Bromus inermis*	*Centaurea maculosa*	*Cirsium arvense*
1	0	0	0	0	0
2	0	0	0.101	1.901	0
3	0	0	0	0	0
4	0	0	0.041	0.021	0
5	0	0	0	0	0
6	0	0	0.2	0	0
7	0	0	0	0	0
8	0	0	0	0	0
9	0	0	0	0	0
10	0.11	0	0	0	0
11	4.18	0	1.25	0	0
12	0.33	0	0	0	0
13	0	0	0	0	0
14	0	0.301	0	0	0
15	0.001	0	0	0	0
16	13.4	0	2.55	0	0
17	11.1	0	5.6	0	10
18	0	0	0.02	0	0
19	0	0	0	0	0
20	0	0	0	0	0
21	0.001	0	0	0	0
22	0	0	0	0	0
23	0	0	0	0	0
24	0.05	0	0	0	0
25	1.7	0.22	14	0	0.02
26	0	0	0.07	3.9	0
27	2.22	0	0	0	0
28	0	0	0	0	0
29	0	0	0	0	0
Function	C3 clonal grass	Biennial Forb	C3 clonal grass	Biennial Forb	Perennial Forb
I-Rank	High	High	High	High	High
Lists	MI,WI,MN,	ALL	ALL (-IN, ON)	ALL (-ON)	ALL (-ON)
Criteria	A	A	A	A	A
mean	1.141	0.018	0.822	0.201	0.346
max	13.4	0.301	14	3.9	10

Table S4.1. (cont'd)

Site	*Dactylis glomerata*	*Hieracium spp.*	*Hypericum perforatum*	*Lonicera spp.*	*Melilotus spp.*
1	0	0	1.1	0	0
2	0	0.041	0.251	0	0
3	0	0	0	0	0
4	0	0.011	0	0	0
5	0	0	0	0	0
6	0	0	0	0.02	0
7	0	0	0	0	0
8	0.1	0	0	0	0.01
9	0	0	0.56	0	0
10	0	0.025	0	0	0
11	0	0	0	0	0
12	0	0	0.3	0	0
13	0	0	0	0	0
14	0	0.08	0	0	0
15	0	0	0	0	0
16	0	0.1	0	0	0
17	0	0	0	0	0
18	0	0	0	0	0
19	0	0	0	0	0
20	0	0	0	0	0
21	0	0	0	0	0.14
22	0	0	0	0	0
23	0	29.5	0	0	0
24	0	0	0	0	0
25	7.6	0	0	0	0
26	0	0	0	0	0
27	0	0	0	0	0
28	0	0	0	0	0
29	0	0	0	0	0
Function	C3 bunch grass	Perennial Forb	Perennial Forb	Shrub/Tree	Leguminous Forb
I-Rank	Medium	Medium	High	High	Medium
Lists	NONE	MI, WI, MN	MI, WI, IN, IL	ALL	ALL (-ON)
Criteria	B	A	A	A	A
mean	0.266	1.026	0.076	0.001	0.005
max	7.6	29.5	1.1	0.02	0.14

Table S4.1. (cont'd)

Site	*Morus alba*	*Phalaris arundinacea*	*Phleum pratense*	*Poa pratensis*	*Rhamnus frangula*
1	0	0	0	3	0
2	0.44	0	0	7.501	0.06
3	0	0	0	0	0
4	0	0.082	0.001	0.083	0
5	0	0	0.16	0.02	0
6	0	0	0	11.9	0
7	0.2	0	0	0	0
8	0	0	0	2.05	0
9	0	0	0	14	0
10	0.4	0	0	38.5	0
11	0	0	0	0	0
12	0	0	0	7.321	0
13	0	0	0	0	0
14	0.3	0	0	0.13	0
15	0.01	0	0	34.5	0
16	0	0	0	53.3	0
17	0	0	0	31.3	0
18	0	0	0	2.2	0
19	0	0	0	2.65	0
20	0	0	0	0.03	0
21	0	0	0	4.7	0
22	0	0	0	0	0
23	0	0	0	0.03	0
24	0	0	0	0.1	0
25	0.04	0	0	6.4	0
26	0	0	0	21.3	0
27	0	0	0	0	0
28	0	0	0	0	0
29	0	0	0	0	0
Function	Shrub/Tree	C3 clonal grass	C3 bunch grass	C3 clonal grass	Shrub/Tree
I-Rank	High	High	Medium	Medium	High
Lists	WI, IN, IL	ALL (-ON)	MI	MI, IL	ALL
Criteria	A	A	B	A	A
mean	0.048	0.003	0.006	8.311	0.002
max	0.44	0.082	0.16	53.3	0.06

Table S4.1. (cont'd)

Site	*Rosa multiflora*	*Trifolium hybridum*	*Trifolium pratense*	*Trifolium repens*
1	0	0.001	0	0
2	0	0	0	0
3	0	0	0	0
4	0	0	0	0.011
5	0	0.012	0	0.002
6	0	0	2.26	0
7	0	0	0	0
8	0.001	0	3.06	0
9	0	0.32	0	0
10	0	0	0.07	0.171
11	0	0.08	0	0.01
12	0	0	0	0
13	0	0	0	0.001
14	0	0	0	0
15	0	0	0.01	0
16	0	0	0.013	0
17	0	0	0.01	0
18	0	0	0	0
19	0	0	0	0
20	0	0	0	0.102
21	0	0	33.5	0.16
22	0	0	0	0
23	0	0	0	0
24	0	0	0	0
25	0	5.92	0	0
26	0	0.06	0	0
27	0	0.02	0	0
28	0	0	0	0
29	0	0	0	0
Function	Shrub/Tree	Leguminous Forb	Leguminous Forb	Leguminous Forb
I-Rank	Medium	Medium	Low	Medium
Lists	ALL (-ON)	NONE	MI	MI
Criteria	A	B	B	B
mean	0	0.221	1.342	0.016
max	0.001	5.92	33.5	0.171

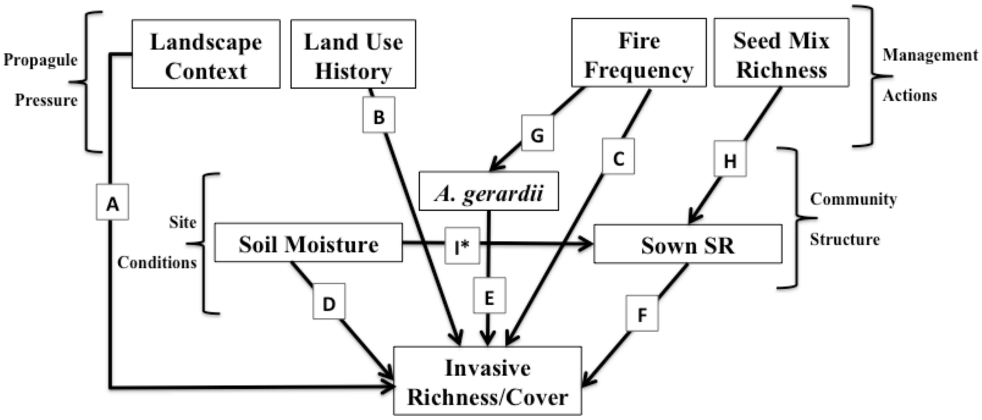
Table S4.1. (cont’d)

Site	Invasive Cover	Sown Cover	Invasive SR	Sown SR
1	4.1	51.15	3	6
2	10.3	49.33	7	8
3	0	34.46	0	7
4	0.25	41.84	7	3
5	0.19	26.1	4	3
6	14.38	74.92	4	29
7	0.2	79.71	1	17
8	5.22	57.53	5	26
9	14.88	50.78	3	17
10	39.28	45.88	6	15
11	5.52	53.36	4	15
12	7.95	55.44	3	18
13	0.001	59.31	1	17
14	0.81	36.87	4	12
15	34.52	49.97	4	13
16	69.36	13.55	5	7
17	58.01	25.71	5	12
18	2.22	70.3	2	15
19	2.65	48.02	1	9
20	0.13	61.36	2	14
21	38.5	36.18	5	12
22	0	52.5	0	12
23	29.53	35.36	2	5
24	0.15	35.32	2	18
25	35.9	45.5	8	17
26	25.33	59.13	4	15
27	2.24	86.52	2	22
28	0	31.52	0	18
29	0	46.84	0	15
mean	13.85	48.77	3.24	13.69
max	69.363	86.52	8	29

Table S4.2. Goodness-of-fit metrics for structural equation models from main text and supplementary information. Definition of metrics (with recommended cutoffs in parentheses): *GFI*=goodness-of-fit index (≥0.90), *NNFI*=nonnormed fit index (≥0.95), *CFI*=comparative fit index (≥0.95), *SRMR*=standardized root mean square residual (≤0.08), *RMSEA*=root mean square error of approximation (≤0.06), *CHISQ*=Chi-square (N/A), *p*=p-value for Chi-square test (>0.05), *df*=degrees of freedom for Chi-square test (N/A). *SEM*=figure associated with model.

Response	gfi	nnfi	cfi	srmr	rmsea	chisq	p	df	R^2	SEM
Invasive richness	0.99	0.86	0.93	0.06	0.12	12.53	0.19	9	0.46	Fig. 4.1a
Invasive cover	0.99	0.94	0.97	0.07	0.09	11.16	0.27	9	0.78	Fig. 4.1b
P. pratensis	0.98	0.91	0.95	0.06	0.09	11.15	0.27	9	0.45	Fig. 4.3a
Trifolium spp.	0.98	0.92	0.96	0.06	0.10	11.50	0.24	9	0.68	Fig. 4.3b
Invasive forbs	0.98	0.87	0.94	0.06	0.10	11.76	0.23	9	0.32	Fig. 4.3c
Exotic richness	0.99	0.89	0.94	0.06	0.10	11.67	0.23	9	0.38	Fig. S4.3a
Exotic cover	0.99	0.94	0.97	0.06	0.10	11.45	0.25	9	0.78	Fig. S4.3b
Row crops	1.00	1.54	1.00	0.04	0.00	0.93	0.92	4	0.30	Fig. S4.4a
Grasslands	1.00	1.18	1.00	0.02	0.00	0.55	0.91	3	0.56	Fig. S4.4b

Figure S4.1. Meta-model visualizing predictions shown in Table 4.1. * path suggested by modification indices.



A. Some land cover types (e.g., agriculture) may support smaller invasive species populations than others (e.g., forest, grassland) and therefore contribute invasive propagules at lower rates (Gifford and Otfinowski 2013).

B. Differences in historical land management (row crops vs. perennial grasslands) select for different types and abundances of invasive species in the seedbank and budbank (Zylka et al. 2016).

C. Fire increases light availability but decreases soil nutrient availability, so may increase or decreasing invasibility. The response of individual species to fire also varies - so the response of specific invaders may vary (Howe et al. 1994).

D. Sites with lower resource availability (here, primarily soil moisture, a key driver of community dynamics in grassland) are more difficult to invade (Davis et al. 2000, Melbourne et al. 2007).

E. Sites dominated by a single highly competitive species may be more resistant to invasion; *A. gerardii* may draw down resources more effectively than a diverse community (Smith et al. 2004).

F. The establishment of a diverse community of sown native species confers biotic resistance; diverse communities of resident species occupy available resources more efficiently (e.g., complementarity) (Kennedy et al. 2002, Levine et al. 2004).

G. More frequent fire, particularly spring fires, may increase dominance by *A. gerardii* (Howe et al. 2011), which **[G > E]** may increase the invasion resistance of the sown community..

H. Sowing more species increases the richness of the sown community (Grman et al. 2013), which **[H > F]** may increase the invasion resistance of the sown community.

I. Sites with lower resource availability may also limit invasion by sown species (Grman and Brudvig 2014), which **[I > F]** may reduce the invasion resistance of the sown community.

Figure S4.2. Abundance of *Andropogon gerardii* is correlated with *A. gerardii seeding rate.*

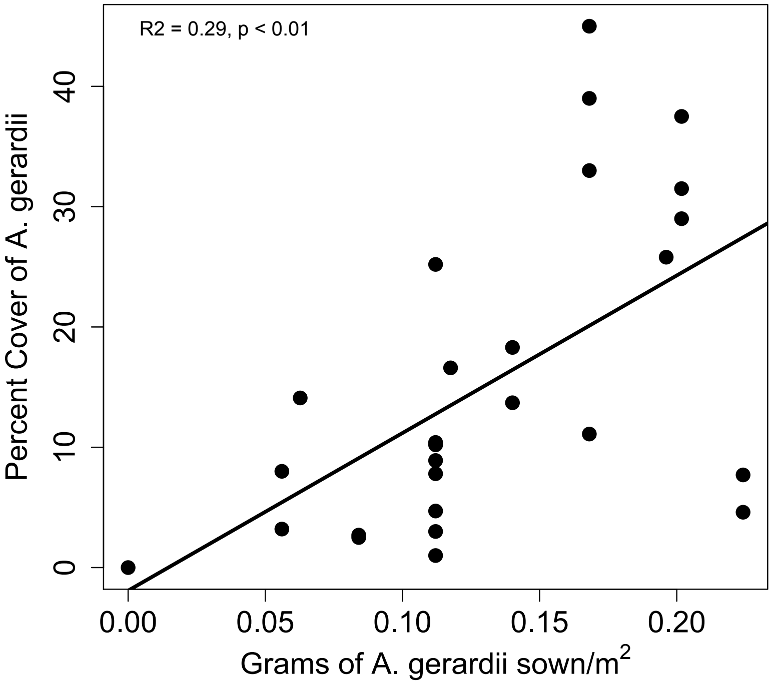


Figure S4.3. Structural equation model showing effects on the richness (a) and percent cover (b) of ALL exotic species. Management (fire frequency, seed mix richness), propagule pressure (landscape context, land-use history), resource availability (soil moisture), and sown community structure (*A. gerardii* abundance, sown species richness) Compare to Figure 4.2, the SEM for only the *invasive* exotic species.

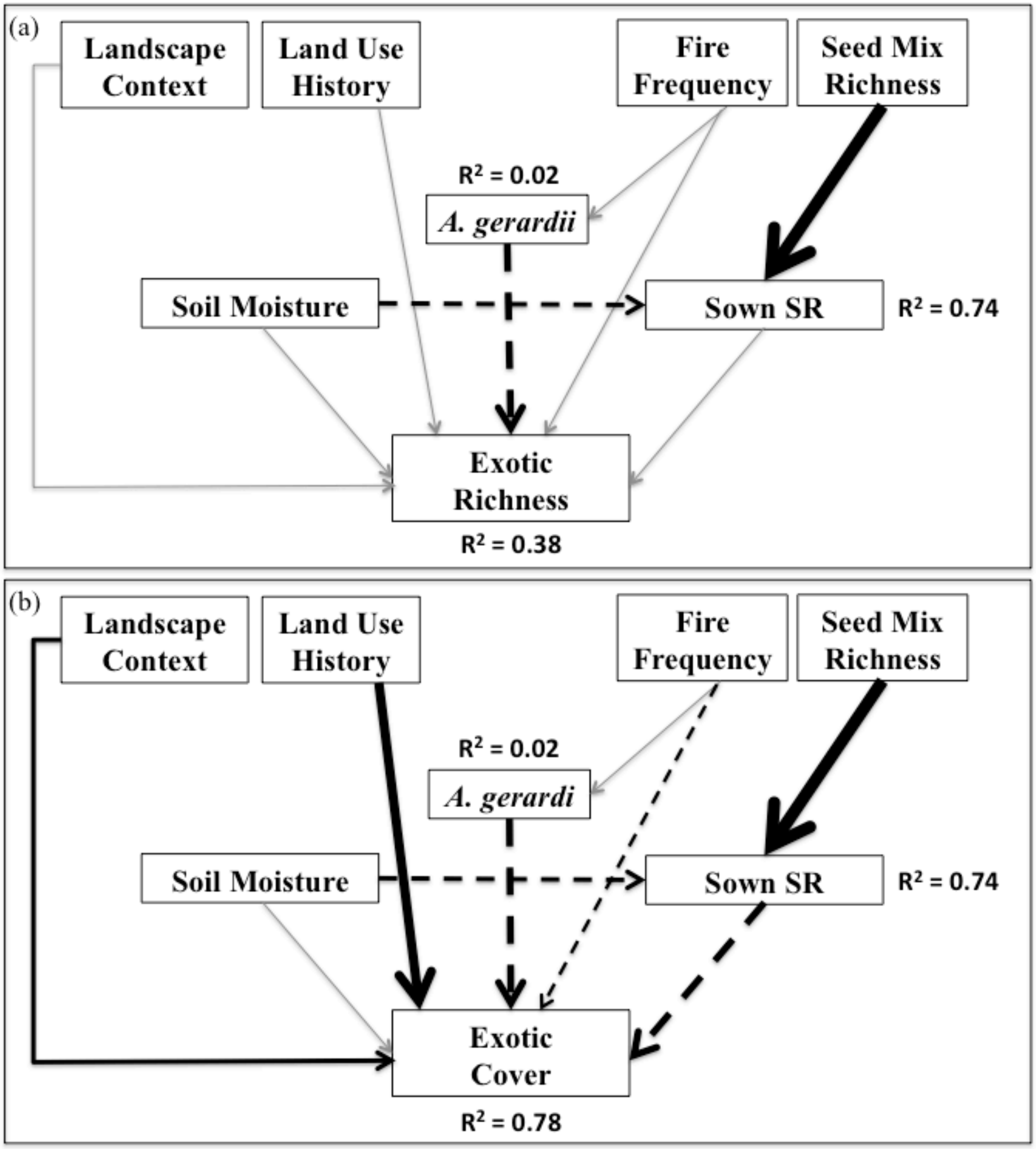
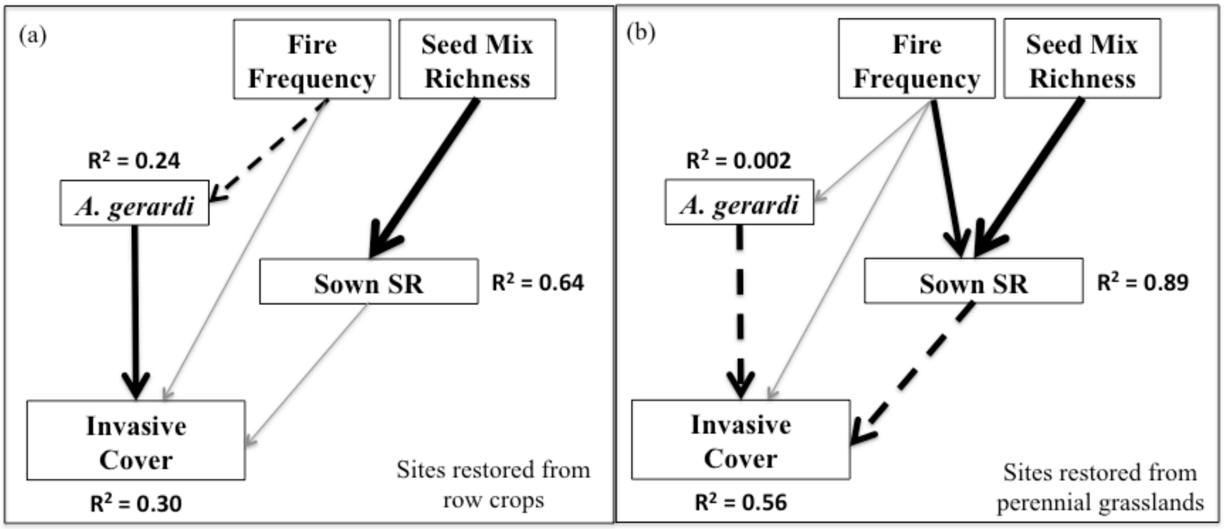


Figure S4.4. The direct and indirect effects of management (fire frequency, seed mix richness) on invasive cover differ by land-use history. Management explained little variation ($R^2 = 0.30$) in cover of invasive species in sites restored from row crops (a). Cover of the sown dominant *A. gerardii* increased invasive cover, but fire frequency indirectly reduced invasive cover by reducing the cover of *A. gerardii*. Management explained more variation ($R^2 = 0.56$) in sites restored from perennial grasslands (b). Both fire frequency and seed mix richness reduced invasive cover by increasing sown species richness.



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